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Redescription of tropical-temperate cladocerans *Alona diaphana* King, 1853 and *Alona davidi* Richard, 1895 and their translocation to *Leberis* Smirnov, 1989 (Branchiopoda: Anomopoda: Chydoridae)

Переописание тропических ветвистоусых ракообразных *Alona diaphana* King, 1853 и *Alona davidi* Richard, 1895 и их перенос в род *Leberis* Smirnov, 1989 (Branchiopoda: Anomopoda: Chydoridae)

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KEY WORDS: Cladocera, Anomopoda, Chydoridae, *Leberis*, systematics, morphology, redescription

КЛЮЧЕВЫЕ СЛОВА: Cladocera, Anomopoda, Chydoridae, *Leberis*, систематика, морфология, переописание

ABSTRACT. A comparison between populations of the *diaphana*-group of *Alona* Baird, 1843 from Australia and America confirms that Australian *A. diaphana* King, 1853 and American *A. davidi* Richard, 1895 are separate species rather than synonyms. Their trunk limb morphology is here studied for the first time.

Both species differ by size, the number of setae on the ventral margin of valves, and numerous details of trunk limb and postabdominal morphology. They share a number of characters, such as an ovoid body shape, dorsal keel and blunt rostrum, separating them from other *Alona* and suggesting a relation with *Celsinotum* Frey, 1991 and *Leberis* Smirnov, 1989. Comparison of their morphology with that of the only species of the latter genus, *L. aenigmatosa* Smirnov, 1989, reveals that differences are of species rather than of generic level. Therefore, both *A. diaphana* and *A. davidi* are relocated to *Leberis*, with small adjustments of the genus diagnosis.

РЕЗЮМЕ. Сравнение австралийских и американских популяций группы видов *diaphana* рода *Alona* Baird, 1843 показало, что австралийский таксон *A. diaphana* King, 1853 и американский таксон *A. davidi* Richard, 1895 являются самостоятельными видами, а не синонимами. Впервые исследована морфология торакальных конечностей этих видов.

Эти виды различаются размерами, числом щетинок на нижнем крае створок, и многими деталями строения торакальных конечностей. Они обладают рядом общих признаков, таких как округлая форма тела, спинной киль, тупой рострум, надежно отделяющих их от видов рода *Alona* и указывающих на близкое родство с родами *Celsinotum* Frey, 1991 и *Leberis* Smirnov, 1989. Сравнение их морфологии с таковой единственного вида рода *Leberis*, *L. aenigmatosa* Smirnov, 1989, показало, что эти виды различаются только признаками видового уровня. Поэтому *A. diaphana* и *A. davidi* переносятся в род *Leberis*.

Introduction

Members of the *Alona diaphana* species group include tropical taxa, markedly different in morphology from the majority of *Alona*, having an ovoid body with clear dorsal ridge and convex ventral margin, a blunt truncated rostrum and a peculiar shape and armament of the postabdomen. Species of this group inhabit freshwaters throughout Australia, Tropical and Subtropical

Asia, Southern Europe, Africa and South and Central America.

A number of names was applied to species of this group, including *Alona diaphana* King, 1853, *Alona davidi* Richard, 1895, *Alona davidi* var. *iheringi* Richard, 1897; *Alona punctata* Daday, 1898 and *Alona davidi vermiculata* Smirnov & Timms, 1983, and a number of early authors [Sars, 1888, 1901; Daday, 1905, 1910; Biraben, 1939] placed the *diaphana*-group in *Alonella* or *Paralonella* [Birge, 1910].

The first-described species in this group, *A. diaphana*, was found by King [1853] in the neighbourhood of Sydney (Australia), and redescribed by Sars [1988] from Rockhampton, Queensland. After his work, the name *Alonella diaphana* was applied to specimens from both paleotropical and neotropical regions. The initial description [King, 1853 : 260, Pl.8, fig. D] was so inadequate that Smirnov [1971] placed *A. diaphana* as *Incertae Sedis*. Later, it was redescribed by Frey [1991] from Sars' material. He points out that "… **Sars' description of the taxon is now the standard for comparison of what is called *Alona diaphana*.**" [Frey, 1991, p. 13]. His conclusion to retain King's name seemed reasonable and was followed by Alonso & Pretus [1989] and Sinev [2001a]. Frey's redescription of *A. diaphana* is elaborate, but did not include trunk limb morphology. At present, the Australian *A. diaphana* King, 1853 is the only well-described taxon within the group [Korovchinsky, 1996].

A second species, *A. davidi* was described by Richard [1985], from Haiti and named in honor of his brother David, who collected the material. He distinguished it from *A. diaphana* by the somewhat different sculpture of the valves. In 1897, Richard described *Alona davidi* var. *iheringi* from Brazil, distinct from the nominal species in valve sculpture and armature of the postabdomen. This taxon should not be mistaken with *Alona iheringi* Sars, 1901, which belongs in the *costata*-group [Sinev, 2001b], recently renamed *Alona iheringula* Kotov & Sinev 2004.

The reasons for separating *Alona davidi* from *Alona diaphana*, given by Richard [1895] seemed dubious, and Sars [1901], investigating specimens reared from dried mud from Argentina, synonymised it with *A. diaphana* (*Alonella diaphana* in his work), but not all later authors agreed with his opinion.

A year after Richard's description of *Alona davidi* var. *iheringi*, Daday [1898] described another species from the same group, *Alonella punctata*, from Ceylon, a name which was transferred by the same author [Daday, 1910] to the African continent, and later regarded as a variety or subspecies of *Alona davidi* (var. *punctata* in Gauthier [1939] or *A. davidi punctata* in Smirnov [1971]). A long period of confusion followed, with the transfer of names between continents. As the present paper focuses mainly on Australian and American populations of the *diaphana*-species complex, the status of other Asian and African members of this group remains uncertain.

Smirnov [1971] and Smirnov & Timms [1983] believed that all populations of the *diaphana*-group belong to one cosmopolitan species, viz. *Alona davidi*, consisting of the subspecies *A. davidi davidi*, *Alona davidi iheringi* and *Alona davidi punctata* (*A. davidi vermiculata* was described in latter work), differing in valve sculpturing, a dubious character, and in the denticulation of the postabdomen. This division into subspecies was taken over in some regional keys [e.g. Michael & Sharma, 1988], exacerbating confusion. Frey [1991] tackled the cosmopolitan nature of *A. diaphana*, but, aware of the inadequate level of study of non-Australian populations, states: "**But until comparisons are made that demonstrate these various taxa are either conspecific or different, it would be acceptable to label them all as *Alona diaphana***" [Frey, 1991]. The present taxonomic situation of the *diaphana*-group is far from acceptable: we know that specimens similar to the Australian *A. diaphana* are found all over the tropics, but we are unable to state with certainty whether they belong to that species or not, and therefore the status of all other taxa within the group remains uncertain.

Another problem arising with the study of the *diaphana*-group is its phylogenetic position within the Aloninae. For many early authors [Sars, 1888, 1901; Daday, 1905, 1910; Biraben, 1939] differences between members of the *diaphana*-group and 'typical' *Alona* seemed to be of generic level, and they placed them in *Alonella*, at that time defined as poorly as *Alona*, or *Paralonella* [Birge, 1910], an even less well-defined, heterogeneous genus, which should be forgotten (though the name remains). After the phylogenetic significance of the head pores in Chydoridae was demonstrated, and the modern system of subfamilies was established [Frey, 1959; 1967], the position of the *diaphana*-group within *Alona* was never questioned.

The aims of our study are (1) to study American populations of the *diaphana*-group and compare them with *Alona diaphana* King, 1853 from Australia to clarify the taxonomic status of *Alona davidi* Richard, 1895, and (2) to clarify the taxonomic status of the *diaphana*-group within the subfamily.

Material and methods

Our material includes populations of *diaphana*-group from Australia, Mexico, Caribbean Islands, Brazil and Argentina, numbering about 800 specimens. Animals were selected from samples under a binocular stereoscopic microscope, placed on slides (in a drop of a glycerol-formaldehyde mixture) and studied under an optical microscope as complete specimens. Several specimens from each population were dissected for analysis of appendages. About 30 specimens were lyophilised, mounted on an aluminium stub, coated with gold, and examined under a scanning electron microscope. Measurements were conducted using an eye-piece-micrometer, all drawings were made with camera lucida.

ABBREVIATIONS. In list of material: AAK — personal collection of Dr. A. A. Kotov; NNS — Prof.

N. N Smirmnov's collection, deposited in Zoological Museum of Moscow University; ZMOU — Zoological Museum of Oslo University.

In illustrations and text: I–V — thoracic limbs I–V; as — accessory seta of limb I; cbs — copulatory brush seta; e1–3 — endites 1–3 of limb I; ex — exopodites of limbs; IDL — inner distal lobe of limb I; IP — inter-pore distance (distance between anterior and posterior major head pores); ms — male seta; ODL — outer distal lobe of limb I; PP — postpore distance (distance between posterior head pore and posterior corner of head shield), s — sensillum.

Results

Our data show that species of *diaphana*-group should be translocated to the genus *Leberis* and confirms the identity of *Alona davidi* (now *Leberis davidi*) as a separate species.

Genus *Leberis* Smirnov, 1989.

Smirnov, 1989: 51–53; Frey, 1998: 31–42.
Type species *L. aenigmatosus* Smirnov, 1989.

EMENDED DIAGNOSIS. Large or medium sized Aloninae. Body compressed laterally, oval or ovoid, with maximum height at middle of body. Both dorsal and ventral margins of valves concave, more or less developed dorsal ridge or keel present on valves, but not on head shield. Sculpture of valves and head shield well developed. Several posteriormost setae of ventral margin of valves short, naked, spine-like. Head shield of alonine habitus, rostrum short and blunt. Eye larger than ocellus. Three equal major head pores, with narrow connection. Lateral head pores point-like.

Labrum large, labral keel broadly expanded, height of labral keel about two times its maximum width. Anterior margin convex or wavy. Distal part of labral keel rounded. Posterior margin of keel slightly convex to straight. No setulation on anterior and posterior margin of keel.

Postabdomen of moderate length and width, narrowing distally. Ventral margin straight. Distal margin either almost straight, perpendicular to ventral one, with dorso-distal angle broadly rounded, or convex, evenly passing into dorsal margin with no clear dorso-distal angle. Dorsal margin straight in postanal portion, weakly concave in anal zone. Preanal angle clearly defined, postanal angle from well-defined to weakly defined, provided with 12–20 groups of small marginal denticles or marginal setules, and 10–15 well-developed lateral fascicles of setules. Postabdominal claw of moderate length, longer or equal to preanal portion of postabdomen, with basal spine, length exceeding width of claw base.

Antennule elongated, not reaching tip of rostrum, with nine terminal aesthetascs. Antennular sensory seta slender, arising sub-distally, about half as long as antennule. Antenna with elongated branches, antennal formula — setae 0-0-3/1-1-3, spines 1-0-1/0-0-1. Basal segments of exopod and endopod twice longer than terminal segment. Length of basal spine of exopod not less than 2/3 of length of middle segment. Terminal spines of antennae shorter than terminal segments.

Five pairs of trunk limbs. Trunk limb I with well-developed accesory seta, one ODL and two IDL, sometimes third rudimentary seta on IDL laterally. Maxillar process with one seta. Trunk limb II with elongated exopodite without seta. Eight scraping spines. Spines 6–8 short, subequal in length, spines 1–5 long, increasing progressively in length distally. Filter plate with seven setae. Exopodites of limb III–V with 6, 4 and 4 setae, respectively. Gnatobase filter plates III–IV with 7–9, 5 and 0 setae, respectively.

Male with body more elongated than female. Postabdomen closely resembling that of female, with clusters of setae in place of female marginal denticles. Sperm duct openings close to base of postabdominal claws. Postabdominal claw shorter than that of female, with well-developed basal spine. Antennula of variable morphology, with 9 or 12 terminal aestetascs and 0, 2 or 4 lateral aestetascs. Trunk limb I with copulatory hook of usual morphology, IDL with male seta equal or longer than other IDL setae.

KEY TO THE SPECIES OF *LEBERIS* (PARTHENOGENETIC FEMALES)

1. Distal margin of postabdomen convex, evenly passing into dorsal margin with no clearly defined dorso-distal angle. Length of adult female 0.8–1.1 mm .... *L. aenigmatosus* Smirnov, 1989
— Distal margin of postabdomen almost straight, perpendicular to ventral margin, with dorso-distal angle broadly rounded. Length of adult female less than 0.7 mm 2
2. Seta of basal segment of exopod of antenna longer than second segment. PP less than 1 IP. Epipodites III–V without finger-like projections. Length of adult female 0.38–0.57 mm .... *L. diaphanus* (King, 1853)
— Seta of basal segment of exopod of antenna shorter than second segment. PP = 1.5–2 IP. Epipodites III–V with long finger-like projections. Length of adult female 0.53–0.77 mm .... *L. davidi* (Richard, 1895)

Leberis aenigmatosus Smirnov, 1989
Figs 1–13.

Smirnov, 1989: 51–53, fig. 1–11; Frey, 1998: 31–42, fig. 1–44.

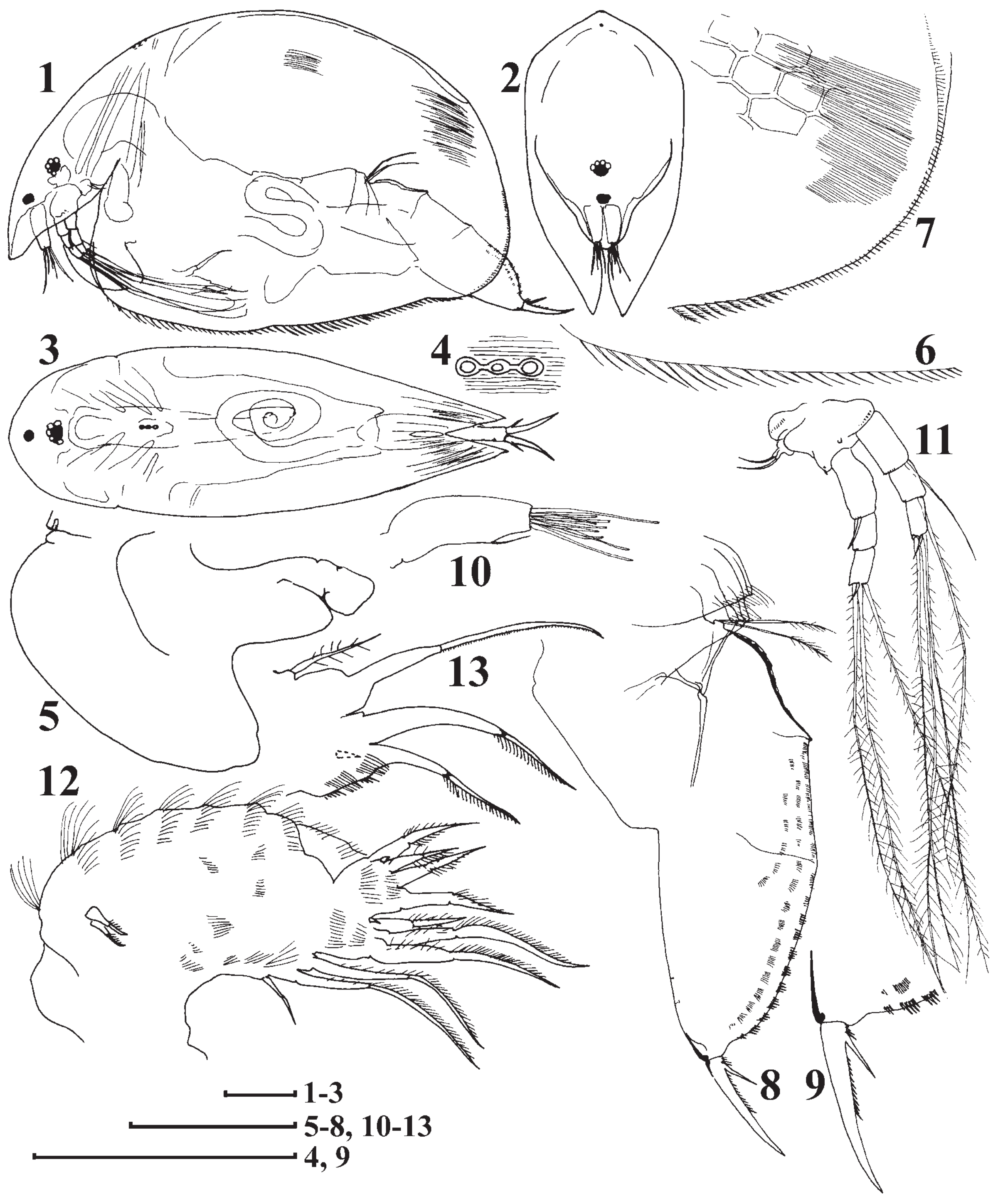
MATERIAL. Australia: 8 parthenogenetic ♀♀ from Western Australia, a pool 28 km West of York, 09.09.1982, coll B. V. Timms.

DIAGNOSIS. Largest *Leberis*, length of adult female up to 1.1 mm. Body as for genus, dorsal ridge weakly developed (Figs 1–3). Valves with 101–129 ventral setae (Figs 6, 7). Postero-ventral portion of valves sculptured, but not head shield. Head shield and head pores as for genus (Fig. 4), PP = 3–4 IP, lateral head pores located about 2 PP from midline. Labrum as for genus, anterior margin of keel always convex (Fig. 5).

Postabdomen with convex distal margin evenly passing into dorsal with no clearly defined dorso-distal angle (Figs 8, 9). Preanal angle clearly defined, postanal angle weak, provided with 12–16 groups of marginal setules, and 10–15 well-developed lateral fascicles of setules. Postabdominal claws as for genus.

Antennule and antenna as for genus (Figs 10, 11). Spine on basal segment of antenna exopod short, about 2/3 length of second segment.

Accessory seta of limb I long, two times shorter than ODL seta, IDL with three setae, third rudimentary seta present (Figs 12, 13). Trunk limb II as for genus. Gnathobase filter



Figs 1–13. *Leberis aenigmatosus* Smirnov, 1989, parthenogenetic ♀♀ from Australia, Western Australia, a pool 28 km West of York, 09.09.1982, coll B. V. Timms: 1–3 — adult in lateral, anterior and dorsal view; 4 — major head pores; 5 — labrum; 6–7 — anterior and posterior portions of valve margin; 8–9 — postabdomen and its distal portion; 10 — antennula; 11 — antenna; 12–13 — limb I and its distal part. Scale denote 0.1 mm.

Рис. 1–13. *Leberis aenigmatosus* Smirnov, 1989, партеногенетические ♀♀, Австралия, Западная Австралия, водоем в 28 км западнее Йорка, 09.09.1982, колл. B. V. Timms: 1–3 — внешний вид сбоку, спереди и со спины; 4 — главные головные поры; 5 — лябрум; 6, 7 — передняя и задняя часть края створки; 8, 9 — постабдомен и его дистальная часть; 10 — антеннула; 11 — антенна; 12, 13 — нога I и ее дистальная часть. Масштаб 0,1 мм.

plate III with 9 setae. Exopodite III with seta 5 longer than seta 6. Epipodites III–V without finger-like projections.

Male. Shape as for genus. Postabdomen closely resembling that of female. Sperm ducts openings close to base of postabdominal claws, with notch before them. Postabdominal claws as for genus. Antennula with 12 terminal aestetascs and 3 or 4 (see discussion) lateral aestetascs. Trunk limb I with elongated, slender copulatory hook, IDL with male seta longer than other IDL setae.

SIZE. Length of adult ♀ 0.8–1.1 mm, length of adult ♂ 0.66–0.74 mm.

Leberis diaphanus (King, 1853)
Figs 14–59.

King, 1853: 260, Pl.8, fig. D (*Alona diaphana*); Sars, 1888: 47–50, pl. 5, fig. 5–7 (*Alonella diaphana*); Sars, 1896: 43; Smirnov, 1971: fig. 430a (*Alona davidi iheringi* partim) Smirnov & Timms, 1983: 40–43 (*Alona davidi*); Frey, 1991: 12–23, fig. 2–41 (*Alona diaphana*)

Type locality: Australia, neighbourhood of Sydney.

Type material: lost.

MATERIAL. Australia: over 200 parthenogenetic ♀♀ from New South Wales, pond near Bondy lake, 10.05.1975, coll. B. Timms, NNS-2000-031; over 40 parthenogenetic ♀♀ from New South Wales, , pond at Tocal via Paterson, 20.06.1967, coll. B. Timms, NNS-2000-028 and NNS-2000-31; over 50 parthenogenetic ♀♀ from Victoria, Swan lake via Porthland, 17.08.1972, coll. B. Timms, NNS-1998-160; over 100 parthenogenetic ♀♀ from Tasmania, Lake Tiberias via Oatlands, 22.08.1974, coll. D. Morton, NNS-2000-127.

DIAGNOSIS. Smallest species of the genus, length of adult female up to 0.57 mm. Body as for genus, dorsal keel well developed. Valves with 58–67 ventral setae. Sculpture of valves and head shield well developed. Head shield and head pores as for genus, PP up to 1 IP, lateral head pores located about 1 PP from midline. Labrum as for genus, anterior margin of keel always convex.

Postabdomen with distal margin practically straight, perpendicular to ventral margin. Preanal and postanal angles clearly defined, provided with 13–17 groups of small marginal denticles and 10–15 well-developed lateral fascicles of setules. Postabdominal claws as for genus.

Antennule and antenna as for genus. Spine on basal segment of antenna exopod long, longer than second segment. Accessory seta of limb I long, twice shorter than ODL seta, IDL with two setae, no third rudimentary seta present. Trunk limb II as for genus. Gnathobase filter plate III with 7 setae. Exopodite III with seta 5 longer than seta 6. Exopodite IV with seta 3 of moderate length, seta 5 longer than seta 6. Epipodites III–V without finger-like projections.

Male. Shape as for genus. Postabdomen closely resembling that of female. Sperm ducts openings above base of postabdominal claws, ventro-distal angle broadly rounded without notch. Postabdominal claws as for genus. Antennula with 9 terminal aestetascs, without lateral aestetascs. Trunk limb I with short, stout copulatory hook, IDL with male seta equal to other IDL setae.

SIZE. Length of adult ♀ 0.38–0.57 mm, length of adult ♂ 0.38–0.4 mm.

DESCRIPTION. Parthenogenetic female. In small females body irregularly ovoid in lateral view (Figs 14, 15). In large females body more regularly ovoid, highly arched, maximum height at middle of body (Figs 15, 24). Maximum height about 0.65–0.76 mm. Dorsal margin uniformly curved, depression between head and rest of body absent, but in most animals dorsal contour slightly broken, somewhat posteriorly to head pores. Postero-dorsal and postero-ventral angles broadly rounded. Posterior margin convex, with step-like depression in ventral portion (Fig. 25). A row of setules along posterior margin at some distance from each other, on the inner side of carapace (Fig. 33, 37); these setules are not organized into groups in the ventral portion of the posterior margin. Ventral margin convex, but wavy due to presence of shallow depressions in medium and posterior portions, with 58–67 setae (Figs 32, 36) of different size in different regions of margin, between them series of small setules (Fig. 31). Last 2–4 setae short, pointed, spine-like. Antero-ventral angle rounded. Sculpture of valves consisting of (Figs 24–27, 35) 18–22 longitudal, sometimes anastomosing lines along all the valves and 7–10 shorter, vertical lines in antero-ventral part of valves.

In dorsal and anterior view, body compressed laterally (Figs 15, 26), with prominent dorsal keel, maximum width of body at level of egg chamber, ventrally width evenly decreasing.

Head relatively small (Figs 27–29), not keeled in anterior view, triangle-round in lateral view, with evenly convex dorsal margin. Rostrum well developed, blunt (Fig. 34). Eye larger than ocellus. Distance from tip of rostrum to ocellus slightly greater than that between ocellus and eye.

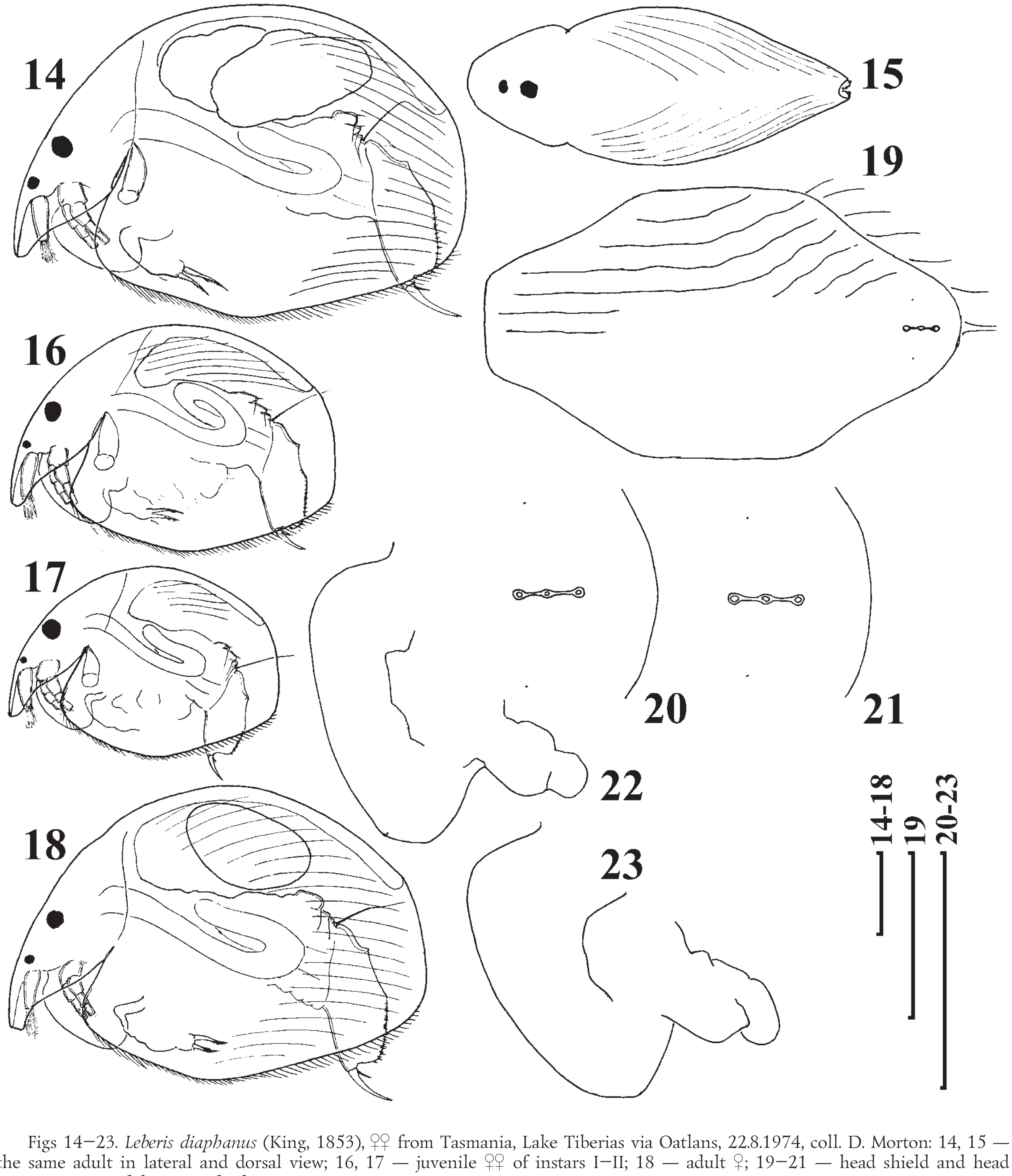
Head shield (Fig. 19) elongated, length about 2.7 times maximum width, its maximum width immediately behind mandibular articulation, with prominent sculpture of mostly longitudal lines. Rostrum short, blunt. Posteriormost extremity of head shield as widely-rounded angle. Three major head pores with narrow connection (Figs 20, 21, 30). Central pore of same size as anterior or posterior one, located at middle. PP less than 1 IP. Minute lateral head pores located far from main pores, about IP distance from midline, at level of central major head pore or somewhat anterior.

Labrum large (Figs 22, 23, 48). Distal labral plate without any setules on sides. Labral keel broadly expanded. Anterior margin convex, not wavy in the majority of adults. Distal part of labral keel rounded in the majority of animals, but sometimes it has expressed, although blunt apex. Posterior margin of keel slightly convex to straight. No setulation both on anterior and posterior margin of keel. A large lateral projection in anterior (basal) portion, and a small hillock in posterior (distal) portion on each side of labrum body. No special folds surrounding its base.

Thorax relatively long. *Abdomen* short, dorsal surface of segments not saddle-shaped. No abdominal projection (although anteriormost segment inflated dorsally), transverse rows of setules on each segment.

Postabdomen relatively broad, slightly narrowing distally, length about 2.5 maximum width. (Figs 38–44). Ventral margin slightly convex to straight, without groups of setules. Inflated basis of claws bordered from distal margin by obscure incision. Distal margin practically straight, broadly rounded angle between distal and dorsal margins. Dorsal margin straight in postanal part, slightly concave in anal part. Distal part, about 3 times longer than preanal one, postanal part 1.5 times longer than anal part. Both preanal and postanal angles well expressed. Preanal margin short, concave in posterior and convex in anterior part, body wall specially chitinized in this region.

Postanal part of the postabdomen provided with 8–11 clusters of marginal denticles (Fig. 45), the distalmost member of cluster always largest. Clusters of denticles evenly passing into groups of marginal setules, the latter have a continuation on anal margin. On sides of postabdomen there



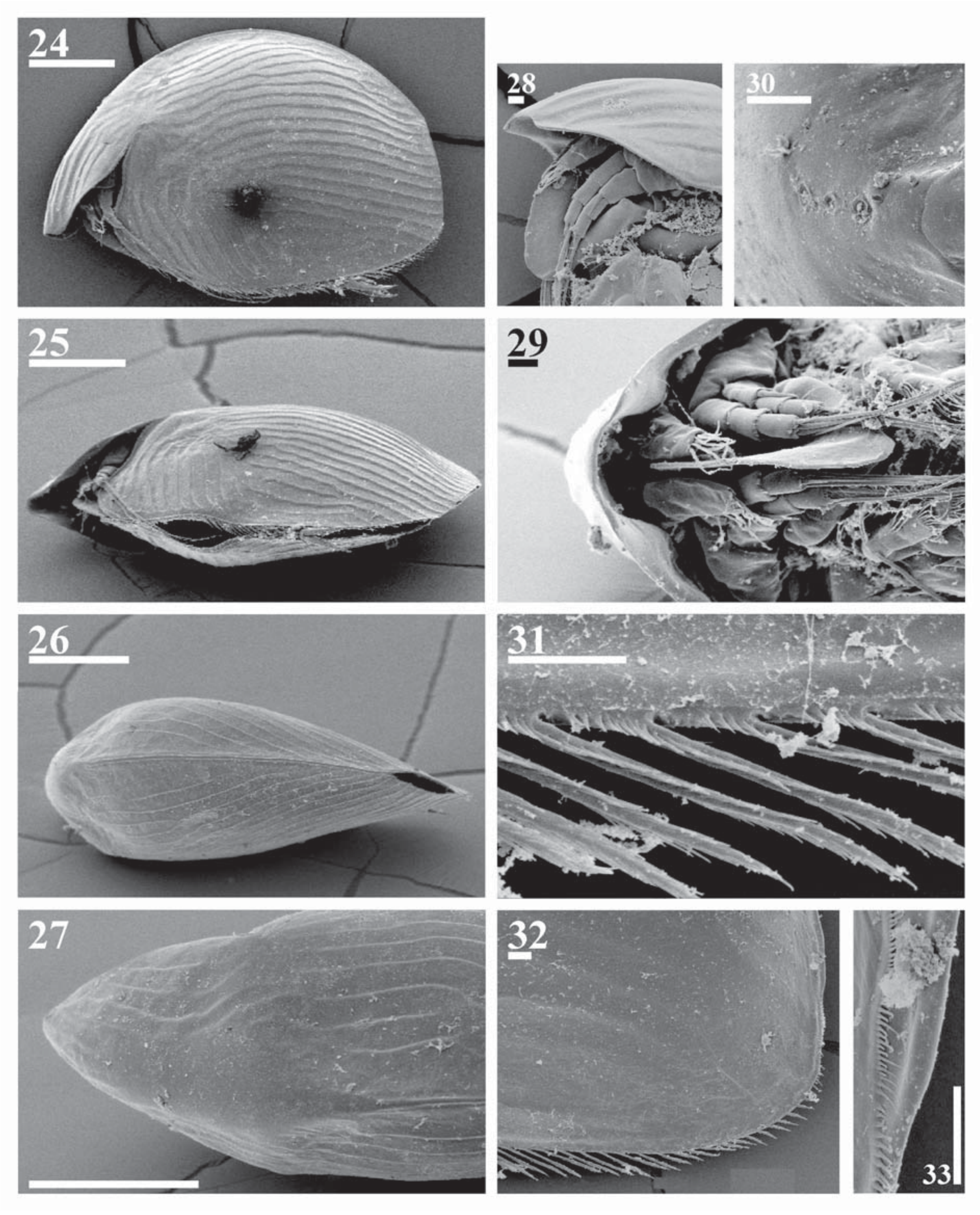
Figs 14–23. *Leberis diaphanus* (King, 1853), ♀♀ from Tasmania, Lake Tiberias via Oatlans, 22.8.1974, coll. D. Morton: 14, 15 — the same adult in lateral and dorsal view; 16, 17 — juvenile ♀♀ of instars I–II; 18 — adult ♀; 19–21 — head shield and head pores; 22, 23 — labrum. Scale denote 0.1 mm.

Рис. 14–23. *Leberis diaphanus* (King, 1853), ♀♀, Тасмания, Lake Tiberias via Oatlans, 22.8.1974, колл. D. Morton: 14, 15 — взрослая партеногенетическая ♀, один и тот же экземпляр сбоку и со спины; 16, 17 — ювенильные ♀♀ первого и второго возраста; 18 — взрослая партеногенетическая ♀; 19–21 — головной щит и головные поры; 22, 23 — лябрум. Масштаб 0,1 мм.

are 11–15 lateral fascicles of relatively long (longer than denticles), delicate setules, distalmost setule of each fascicle longest; additional rows of fascicles in anal region.

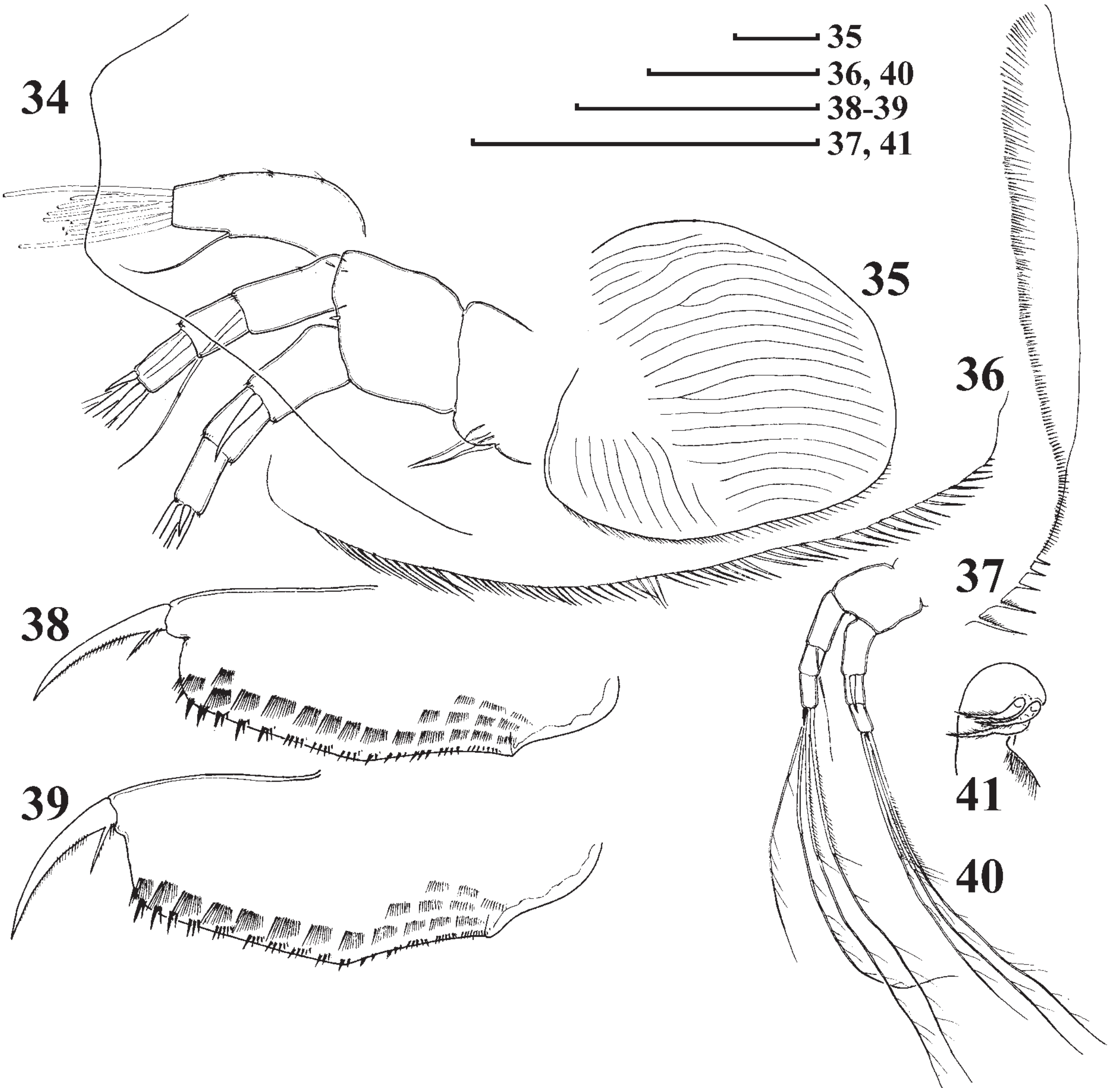
Postabdominal claw relatively short, but not too robust (Fig. 46), longer than preanal portion of postabdomen, with two pectens of setules along dorsal margin, largest of tnem ending before the claw length. Basal spine ca. 0.30–0.35 mm as short as claw proper, armed by short setules along dorsal margin. Cluster of two-three long setules at claw base.

Antennule relatively elongated, not reaching the tip of rostrum, with 3 transverse rows of very short setules at anterior face (Figs 34, 48). Antennular sensory seta slender, arising sub-distally (relatively far from bunch of esthetascs), shorter than antennule, but projecting markedly beyond the distal antennular end. Nine aesthetascs, two of them longer



Figs 24–33. *Leberis diaphanus* (King, 1853), parthenogenetic ♀♀ from Tasmania, Lake Tiberias via Oatlands, 22.8.1974, coll. D. Morton: 24–26 — lateral, ventral and dorsal view; 27–29 — head in dorsal, lateral and ventral view; 30 — head pores; 31 — setules between setae at medium portion of valve margin; 32, 33 — armature of postero-ventral and posterior margin of valve. Scale: denote 0.1 mm (24–27) and 0.01 mm (28–33).

Рис. 24–33. *Leberis diaphanus* (King, 1853), партеногенетические ♀♀, Тасмания, Lake Tiberias via Oatlans, 22.8.1974, колл. D. Morton: 24–26 — внешний вид латерально, вентрально и дорсально; 27–29 — голова дорсально, латерально и вентрально; 30 — головные поры; 31 — сетулы между щетинками в центральной части нижнего края створок; 32, 33 — вооружение заднее-нижнего угла и заднего края створок. Масштаб: 0,1 мм (24–27) и 0,01 мм (28–33).



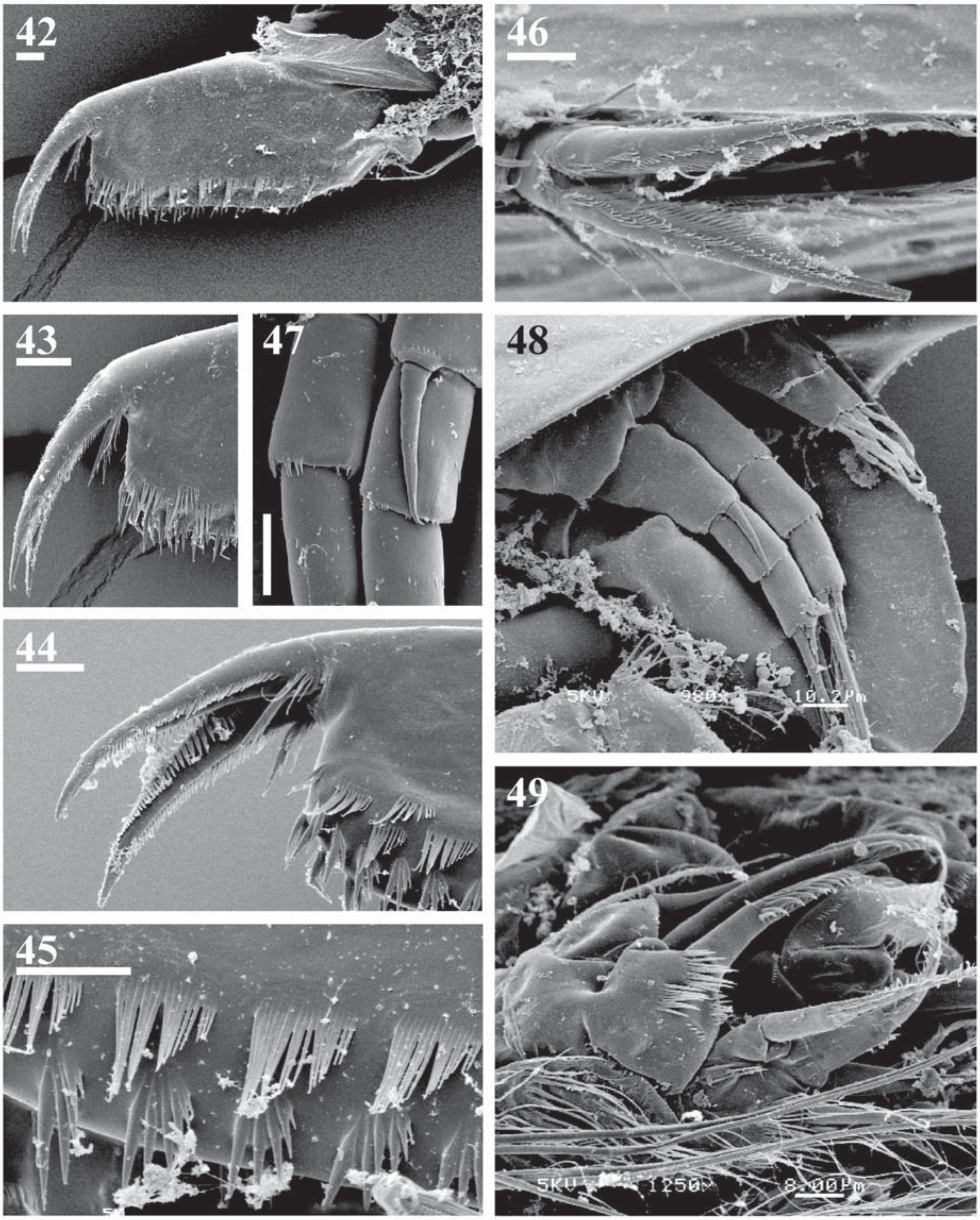
Figs 34–41. *Leberis diaphanus* (King, 1853), parthenogenetic ♀♀ from Tasmania, Lake Tiberias via Oatlands, 22.8.1974, coll. D. Morton: 34 — rostrum, antennula and antenna; 35–37 — valve and its ventral and posterior margin; 38, 39 — postabdomen; 40 — antenna; 41 — maxillula. Scale denote 0.1 mm.

Рис. 34–41. *Leberis diaphanus* (King, 1853), партеногенетические ♀♀, Тасмания, Lake Tiberias via Oatlans, 22.8.1974, колл. D. Morton: 34 — рострум, антеннула и антенна; 35–37 — створка и ее нижний и задний края; 38, 39 — постабдомен; 40 — антенна; 41 — максиллула. Масштаб 0,1 мм.

than the rest, but shorter than antennule. All aesthetascs projecting beyond tip of rostrum.

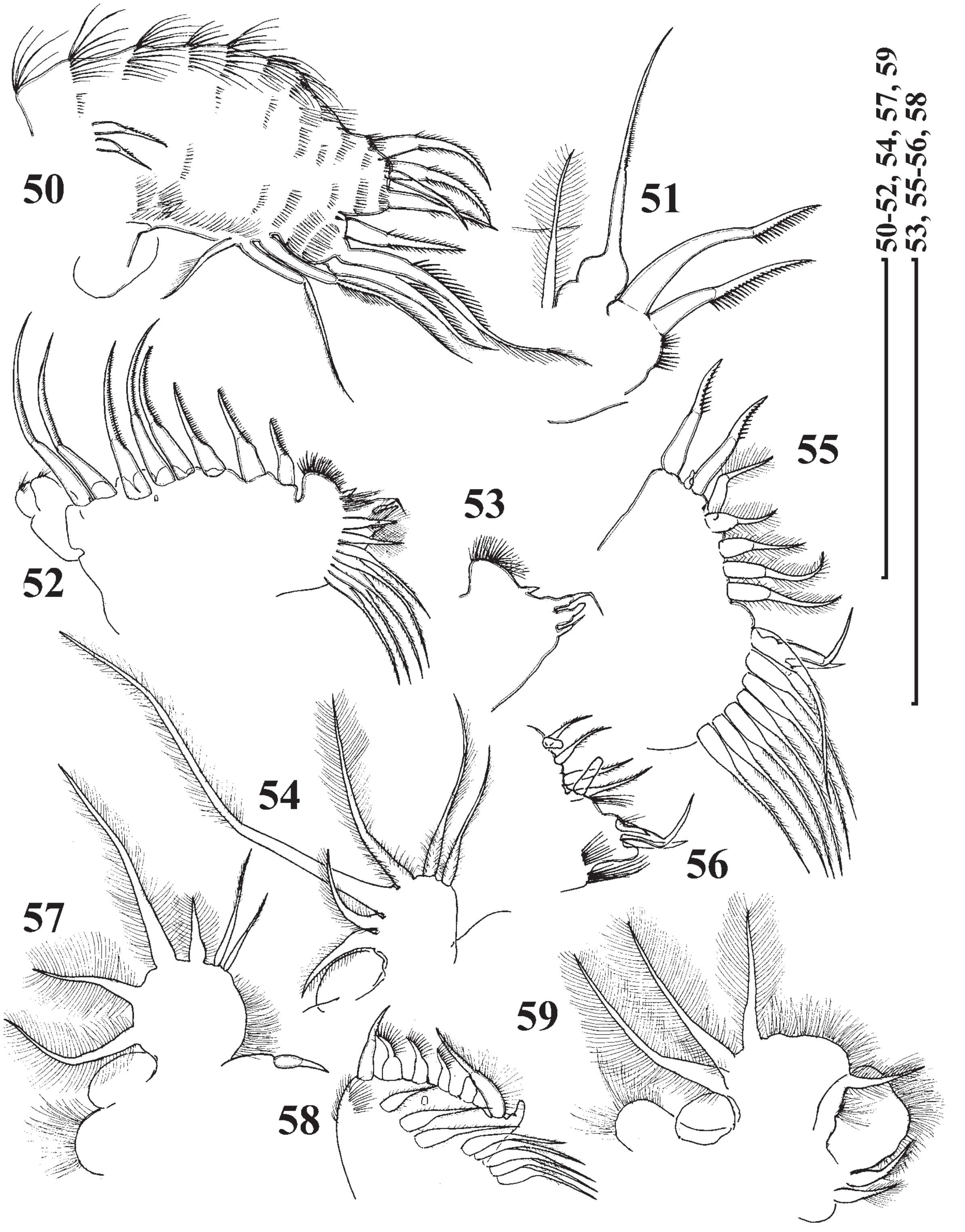
Antenna short (Figs 34, 40, 48). Antennal formula, setae 0-0-3/1-1-3, spines 1-0-1/0-0-1. Coxal part folded, with two sensory setae. Basal segment robust, with rudimentary seta distally. Branches relatively elongated, all segments cylindrical, with minute setules around distal margin, basal segments longest. Apical setae long for a chydorid, setulated asymmetrically. Seta arising from basal segment of endopod thin, short, but projecting beyond tip of distal segment. Seta arising from middle segment of endopod shorter than apical setae. Spine on basal segment of exopod longer than second segment (Fig. 47). Spines from both apical segments of exopod and endopod short, with length less than half that of apical segments.

Trunk limb I large (Fig. 50). Epipodite ovoid, without finger-like projection. Accessory seta long, two times shorter than ODL seta, feathered bilaterally by long setules. ODL with one long, bisegmented seta, distal segment armed unilaterally by short setules. IDL with two setae of unequal length, both armed with hard setules in distal part, and 2–3 clusters of setules on ventral face of IDL (Figs 49, 51).



Figs 42–49. *Leberis diaphanus* (King, 1853), parthenogenetic ♀♀ from Tasmania, Lake Tiberias via Oatlands, 22.8.1974, coll. D. Morton: 42–44 — postabdomen and its distal portion; 45 — distal portion of postanal margin; 46 — postabdominal claws; 47 — branches of antenna; 48 — antennula and antenna; 49 — distal portion of limb I. Scale denote 0.01 mm.

Рис. 42–49. *Leberis diaphanus* (King, 1853), партеногенетические ♀♀, Тасмания, Lake Tiberias via Oatlans, 22.8.1974, колл. D. Morton: 42–44 — постабдомен и его дистальная часть; 45 — дистальная часть постанального края постабдомена; 46 — коготки постабдомена; 47 — ветви антенны; 48 — антеннула и антенна, 49 — дистальная часть ноги I. Масштаб 0,01 мм.



Figs 50–59. *Leberis diaphanus* (King, 1853), thoracic limbs of parthenogenetic ♀♀ from Tasmania, Lake Tiberias via Oatlands, 22.8.1974, coll. D. Morton: 50, 51 — limb I and its distal portion; 52, 53 — limb II and its gnathobase; 54–56 — exopodite, inner portion, and gnathobase of limb III; 57, 58 — exopodite and inner portion of limb IV; 59 — limb V. Scale denote 0.1 mm.

Рис. 50–59. *Leberis diaphanus* (King, 1853), ноги партеногенетических ♀♀, Тасмания, Lake Tiberias via Oatlans, 22.8.1974, колл. D. Morton: 50, 51 — нога I и ее дистальная часть; 52, 53 — нога II и ее гнатобаза; 54–56 — экзоподит, внутренняя часть и гнатобаза ноги III; 57, 58 — экзоподит и внутренняя часть ноги IV; 59 — нога V. Масштаб 0,1 мм.

Endite 3 with four setae of subequal length, one of them lies anteriorly to others, a small sensillum near its base. On endite 2 three densely feathered setae, of unequal size, the longest one larger than ODL seta Endite 1 with three setae, two distalmost members long, bisegmented and setulated in distal part, third seta short and naked. Rows of thin setules on ventral face of limb. Two ejector hooks small, subequal in size. Maxillar process with one short, completely setulated seta.

Trunk limb II triangle-round (Fig. 52). Epipodite as hillock, poor expressed. Exopodite ovoid, without setae, only with rows of fine setules. Inner portion of limb ("endopodite") with eight scraping spines decreasing in length toward gnathobase. Four distalmost members armed with thinner setules, than others. A deep incision between "endopodite" and gnathobase. Portion of gnathobase bordering the "endopodite" somewhat inflated, and densely setulated (Fig. 53). Distal armature of gnathobase with four elements, one of them minute. Filter plate II with seven setae, three posteriormost members shorter than the rest, the posteriormost seta specially inflated.

Trunk limb III. Epipodite ovoid, without finger-like projection. Exopodite sub-quadrangular (Fig. 54), setae on it subdivided into distal and basal groups un-clearly. Seta 3 very long, with massive basal part, setae 4 and 5 two times shorter, other setae three times shorter than seta 3. Setae 1–4 feathered by long setules in distal part, setae 5–6 with short setules in distal part.

Distal endite with three setae, two distalmost stout, with distal segments unilaterally armed with short setules, basalmost seta slightly shorter, unilaterally armed with long setules (Fig. 55). A small bottle-shaped sensillum near medium seta, minute element near seta 3 too. Basal endite with four setae, slightly increasing in size in length in basal direction, all armed distally by short setules. Four soft setae increasing in size basally. Gnathobase unclearly separated from basal endite. Distal armature of gnathobase with four elements (Fig. 56). The first one elongated, bottle-shaped sensillum, second long, but thick seta, third and fourth elements are spine-like setae. Filter plate III with seven setae subequal in size and with similar setulation.

Trunk limb IV. Pre-epipodite setulated, epipodite ovoid, without finger-like projection. Exopodite rounded, with six setae (Fig. 57). Pattern of their location similar to limb III, but armed in different manner. Seta 3 longest, setae 1, 2 and 5 two times shorter, seta 6 three times shorter, and seta 4 four times shorter than seta 3. Setae 1–4 feathered by long setules, setae 5–6 with short setules in distal part.. "Endopodite" IV with four marginal setae (Fig. 58). Distalmost seta stout, armed by short setules distally, three others with inflated basal segments and slender, setulated distal segments. An element (sensillum?) near seta 3. Three soft setae with size increasing basally. Gnathobase with one globular sensillum, medium-sized bisegmented setae, and very short rudimentary seta. Filter plate with five setae.

Trunk limb V. Pre-epipodite ovoid, setulated. Epipodite ovoid, without finger-like projection (Fig. 59). Exopodite trapezium-shaped, lateral group with three densely setulated setae, distally only a single sort seta. Inner limb portion as broad subrectangular lobe, with setulated inner margin. At inner face, two short densely setulated setae, distalmost somewhat larger. No filter plate found.

No males and ephippial females were present in our material, description based on Frey's work [1991].

Ephippial female. Similar in shape to parthenogenetic females. Ephippium weakly pigmented, with well-developed egg locules, covered by polygonal sculpture.

Male. Body shape of both instar I and instar II males similar to that of juvenile females of same instar. Adult male only a little larger than instar II male, of same proportions.

Postabdomen in instar I, similar to that of female, with sperm ducts opening at middle of ventral margin. In instar II, sperm duct openings located closely to base of postabdominal claws, with a notch behind them, angle between distal and dorsal margins of postabdomen almost right. Postabdomen of both juvenile instars armed with same marginal denticles as female postabdomen, with poslabdominal claws resembling those of female. In adult male, postabdomen more narrow than in female, dorso-distal angle of it varies from well-defined, similar to that of female to almost absent, broadly rounded. Both postanal and preanal angles weakly defined. Sperm ducts openings located straight above the base of postabdominal claws. Clusters of short setules located in place of female marginal denticles. Postabdominal claws considerably shorter than that of female, but the length of basal spine remains the same as in female. Setulation of claws and spine same as in female.

Antennule in instar I, same as in female, with nine aesthetascs only. In instar II, antennule with rudimentary male seta, with nine aesthetascs only, but differences in size between them remarkably smaller than in female. In adult male, the number of aesthetascs increase, and two lateral aesthetascs appear under the base of male seta, but due to the poor preservation of aesthetascs we were unable to determinate the number of the terminal ones. Male seta well-developed, about one-third length of antennule.

Trunk limb I in instar I, copulatory hook short and stout, IDL of same structure as in female. In instar II, copulatory hook curved, IDL with anlage of male seta, ventral face of limb with anlage of copulatory brush seta. Two rows of 5–6 long, hard setules in each on ventral face of limb under anlage of copulatory brush setae. In adult male, copulatory hook U-shaped, with free arm little longer than its base, IDL with male seta shorter than both IDL setae, copulatory brush setae of about two third length of male seta. Row of 25–30 long, hard setules on ventral face of limb, continuing from copulatory brush to first seta of endite 3 .

SIZE. Minimal length of juvenile ♀ from 0.28 mm, length of adult ♀ 0.38–0.57 mm, length of adult ♂ 0.38–0.4 mm.

VARIABILITY. No significant interpopulational variability was revealed, and all studied populations were within the limits of variability described by Frey (1991). Variability of antennule, antenna, and trunk limbs was minimal.

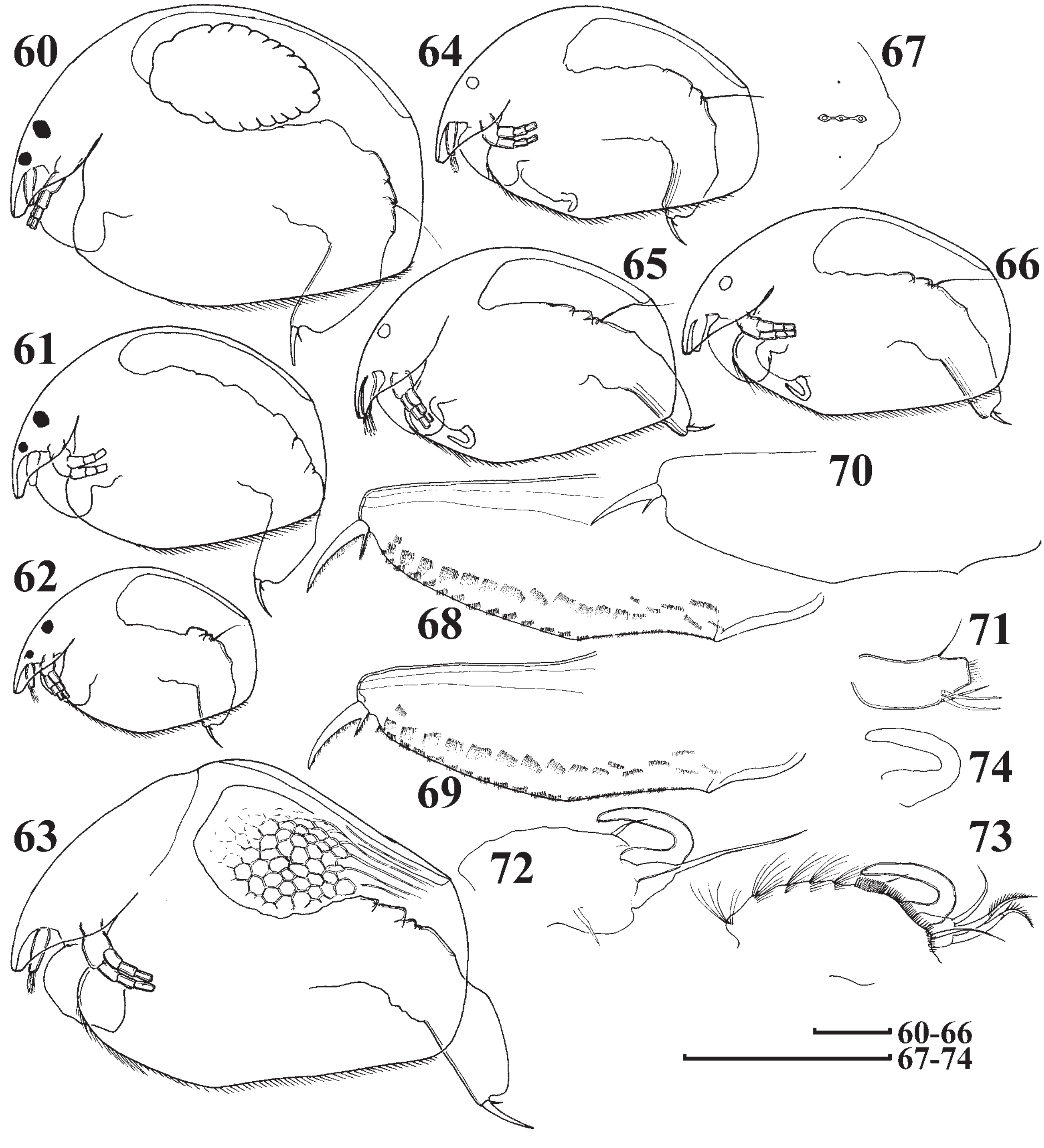
Leberis davidi (Richard, 1895)
Figs 60–150.

Richard, 1895: 192–195, fig. 5–8 (*Alona*); Richard, 1987: 294–296, fig. 42–43 (*Alona davidi* var. *iheringi*); Sars, 1901: 60–61, pl. X, fig. 3, 3a–b (*Alonella diaphana*); Daday, 1905 : 163–164, Taf. X, fig. 12–17 (*Alonella punctata*); Biraben, 1939: 663–665, fig. 17–18 (*Alonella diaphana*); Smirnov 1971: fig. 429a (*Alona davidi davidi* partim); Infante, 1980: 599, fig. 6 (*Alona diaphana*).

Type locality: "…une mare a Brouillard, pres de Port-au-Prince", Haiti.

Type material: lost — not present in Richard's collection (F. Ferrari, personal communication).

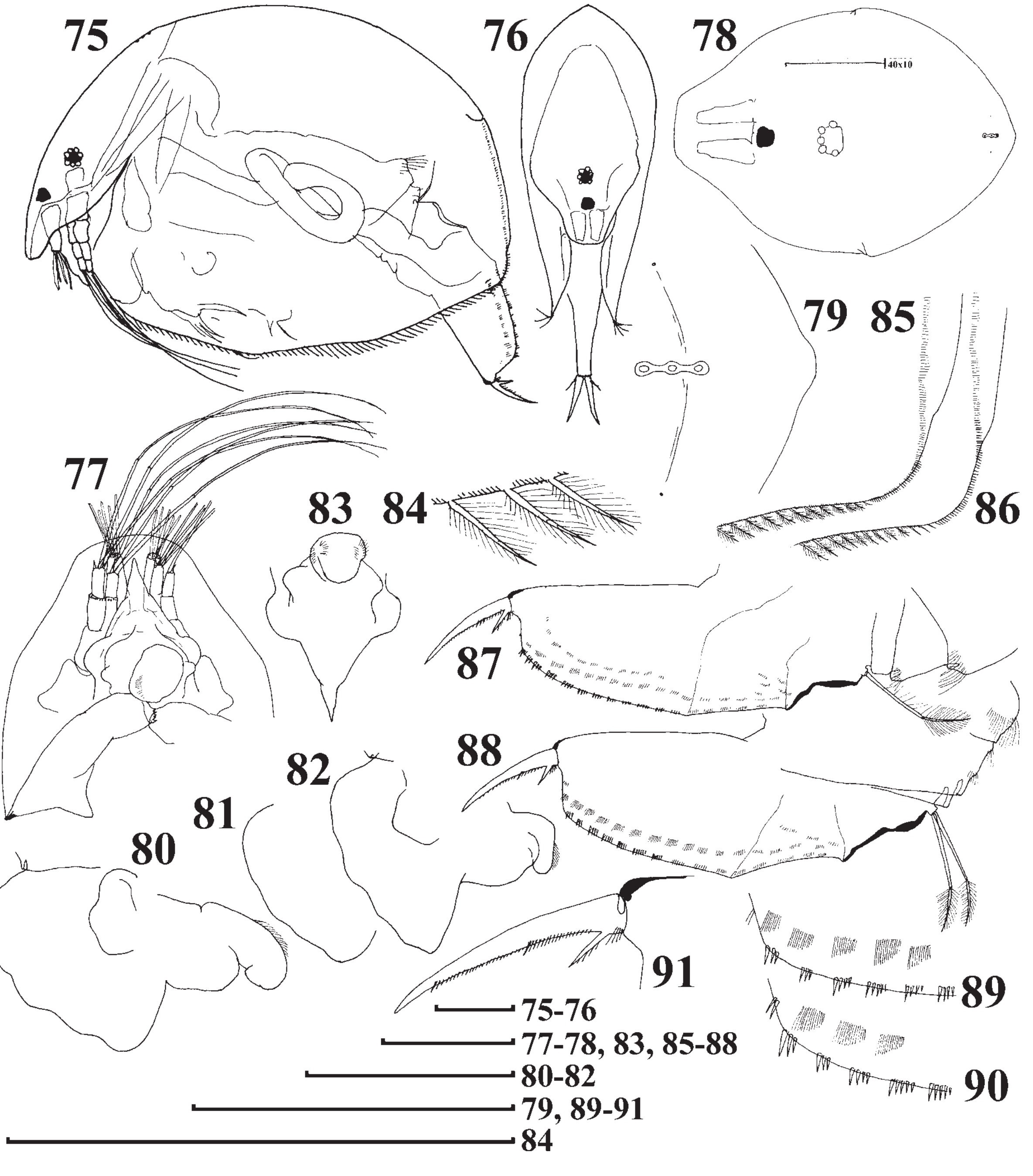
MATERIAL. MEXICO: over 200 parthenogenetic ♀♀ and juvenile ♂♂ from Chiapas, Lagos de Montebello, a small pond near Pojoj, 6.04.2000, coll. M. Gutierrez-Aguirre, AAK; 10 parthenogenetic ♀♀ from Chiapas, a pond at highway Comitan-



Figs 60–74. *Leberis davidi* (Richard, 1895) from Argentina, specimens hatched by G. O. Sars from dried mud, no more precise location known. 60 — large adult parthenogenetic ♀; 61, 62 — juvenile ♀♀ of instar I and II; 63 — ephippial ♀; 64 — juvenile ♂ of instar II; 65–74 — adult ♂: 65, 66 — lateral view; 67 — head pores; 68–70 — postabdomen; 71 — antennula; 72–74 — limb I and copulatory hook. Scale denote 0.1 mm.

Рис. 60–74. *Leberis davidi* (Richard, 1895) из Аргентины, особи выращенные Г. О. Сарсом из высохшего ила, более точное местоположение неизвестно. 60 — крупная взрослая партеногенетическая ♀; 61, 62 — ювенильные ♀♀ первого и второго возраста; 63 — эфиппиальная ♀; 64 — ювенильный ♂ второго возраста; 65–74 — взрослый ♂: 65, 66 — внешний вид; 67 — головные поры; 68–70 — постабдомен; 71 — антеннула; 72–74 — нога I и копулятивный крюк. Масштаб 0,1 мм.

Montebello, 16.04.2000, coll. M. Gutierrez-Aguirre, AAK; 4 partenogenetic ♀♀ from Tabasco, a small pond near Balancan, 30.01.1999, coll. M. Gutierrez-Aguirre, AAK; 7 parthenogenetic ♀♀ from State of Mexico, a small pond at km. 44 of highway Atlacomulco-Toluca (2394 a.s.l.), 11.10.1993, coll. M. Elias-Gutierrez, AAK. CUBA: over 100 parthenogenetic ♀♀ from pond in Guanabo near Havana, 15.10.1987, NNS-1997-187. JAMAICA: 9 juvenile ♀♀ from Black River, no date, coll. W Janetsky, NNS-1999-021. BRAZIL: 25 parthenogenetic ♀♀, 6 ephippial ♀♀, 5 ♂♂, specimens grown from dried mud deriving from temporary dune pools near the village of Atins, Lenchoes Maranhenses National Park, NE-Brazil, 23.12.1997,

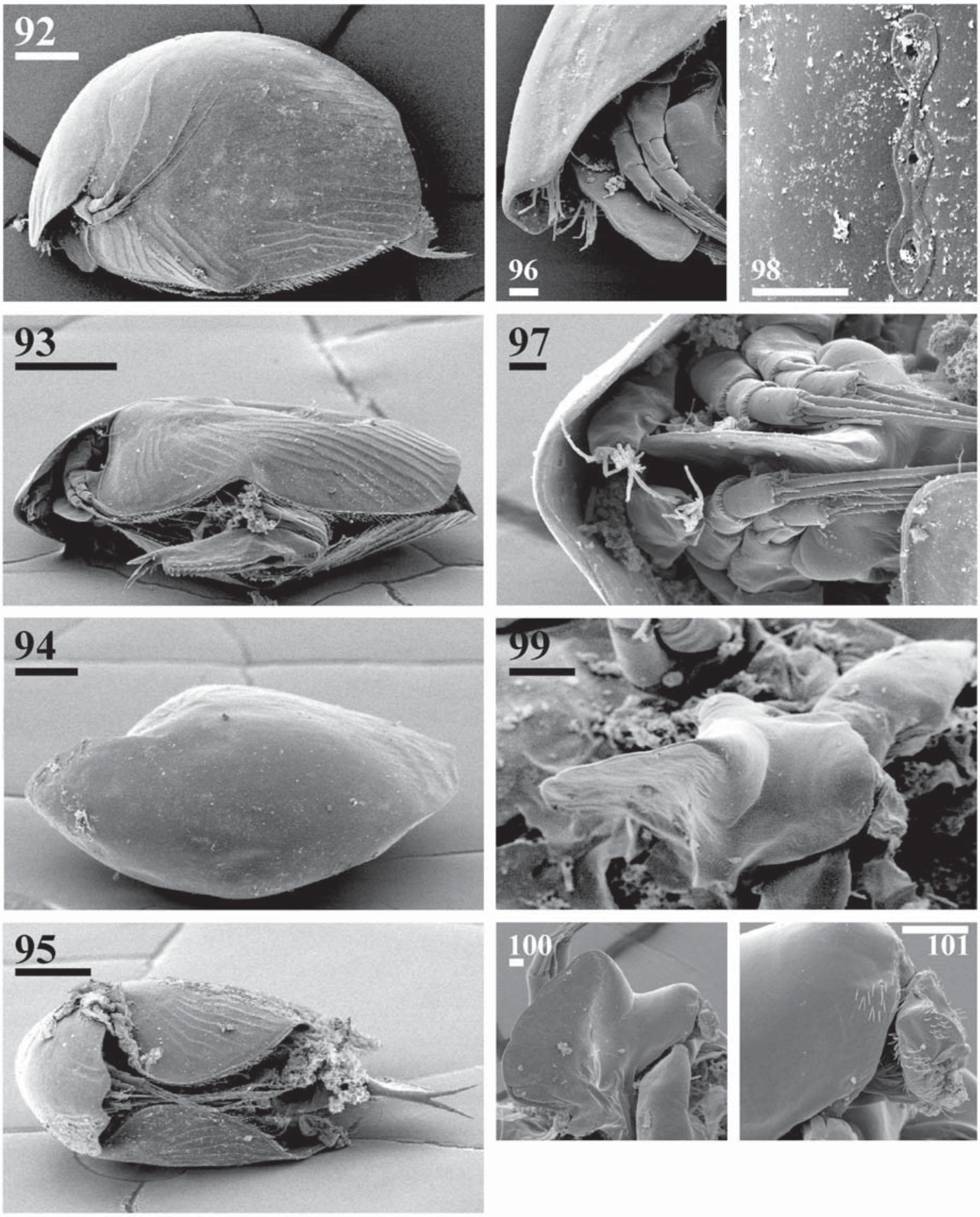


Figs 75–91. *Leberis davidi* (Richard, 1895), parthenogenetic ♀♀ from Mexico, Chiapas, Lagos de Montebello, a small pond near Pojoj, 16.04.2000, coll. M. Gutierrez-Aguirre: 75, 76 — lateral and anterior view; 77 — head in ventral view; 78, 79 — head shield and head pores; 80–82 — labrum view; 83 — labrum in posterior view; 84–86 — armature of ventral and postero-ventral portion of valve; 87, 88 — postabdomen; 89, 90 — its postanal margin; 91 — postabdominal claw. Scale denote 0.1 mm.

Рис. 75–91. *Leberis davidi* (Richard, 1895), партеногенетические ♀♀ Мексика, Чапас, Lagos de Montebello, небольшой пруд в окрестностях Pojoj, 16.04.2000, колл. M. Gutierrez-Aguirre: 75, 76 — внешний вид латерально и спереди; 77 — голова латерально; 78, 79 — головной цит и головные поры; 80–82 — лябрум сбоку; 83 — лябрум сзади; 84–86 — вооружение нижнего края и заднее-нижнего угла створок; 87, 88 — постабдомен; 89, 90 — его постанальная часть; 91 — коготки постабдомена. Масштаб 0,1 мм.

coll. K. Van Damme. ARGENTINA: specimens grown by G. O. Sars from dried mud, no more precise location known: over 60 parthenogentic ♀♀, 17 ephippial ♀♀, 12 ♂♂, 1 juvenile ♂ of instar II, ZMOU, sample F12342; 14 partenogenetic ♀♀, 2 ephippial ♀♀, 1 ♂, ZMOU, sample F12343; 15 partenogentic ♀♀ ZMOU, slide F9103; 22 partenogenetic ♀♀, 11 ephippial ♀♀, 5 ♂♂, 3 juvenile ♂ of instar II , ZMOU, slide F9104; 5 partenogenetic ♀♀, 4 ephippial ♀♀, 1 ♂, ZMOU, slide F9105.

DIAGNOSIS. Of moderate size, length of adult ♀ up to 0.69 mm. Body as for genus, dorsal keel weakly developed.



Figs 92–101. *Leberis davidi* (Richard, 1895), parthenogenetic ♀♀ from Mexico, Chiapas, Lagos de Montebello, a small pond near Pojoj, 16.04.2000, coll. M. Gutierrez-Aguirre: 92–95 — adult ♀ in lateral, ventral, dorsal and anterior view; 96, 97 — head in lateral and ventral view; 98 — major head pores; 99, 100 — labrum in ventral and lateral view; 101 — its posterior portion. Scale denote 0.1 mm (92–95) and 0.01 mm (96–101).

Рис. 92–101. *Leberis davidi* (Richard, 1895), партеногенетические ♀♀ Мексика, Чапас, Lagos de Montebello, небольшой пруд в окрестностях Pojoj, 16.04.2000, колл. M. Gutierrez-Aguirre: 92–95 — взрослая ♀ латерально, вентрально, дорсально и спереди; 96, 97 — голова латерально и вентрально; 98 — главные головные поры; 99, 100 — лябрум вентрально и латерально; 101 — его задняя часть. Масштаб 0,1 мм (92–95) и 0,01 мм (96–101).

Valves with 84–95 ventral setae. Sculpture of valves and head shield moderately developed. Head shield and head pores as for genus, PP = 1.5–2 IP, lateral head pores located about 1.5–2 PP from midline. Labrum as for genus, anterior margin of keel frequently wavy.

Postabdomen with distal margin practically straight, perpendicular to vental one. Preanal and postanal angles clearly defined, provided with 15–20 groups of small marginal denticles and 10–15 well-developed lateral fascicles of setules. Postabdominal claws as for genus.

Antennule and antenna as for genus. Spine on basal segment of antenna exopod long, only somewhat shorter than second segment. Accessory seta of limb I short, three times shorter than ODL seta, IDL with two setae, no third rudimentary seta present. Trunk limb II as for genus. Gnathobase filter plate III with 7 setae. Exopodite III with equal setae 5 and 6. Exopodite IV with very long seta 3, setae 5 and 6 of same length. Epipodites III–V with long finger-like projections.

Male. General shape as for genus. Postabdomen closely resembling that of female. Sperm duct openings above to the base of postabdominal claws, ventro-distal angle broadly rounded without notch. Postabdominal claws as for genus. Antennula with 9 terminal aesthetascs and 2 lateral aesthetascs. Trunk limb I with short, stout copulatory hook, IDL with male seta equal to other IDL setae.

SIZE. Length of adult ♀ 0.53–0.67 mm, length of adult ♂ 0.44–0.52 mm.

DESCRIPTION. Parthenogenetic female. In juveniles, body irregularly ovoid in lateral view (Figs 61, 62, 138). In large females body more regularly ovoid, very high and highly arched, maximum height at middle of body (Figs 60,75, 92). Maximum height about 0.64–0.77 mm length in both juveniles and adults. Dorsal margin generally uniformly curved, depression between head and rest of body absent, but mostly dorsal contour slightly broken posteriorly to head pores. Postero-dorsal and postero-ventral angles expressed, although rounded. Posterior margin generally slightly convex to straight, but with step-like depression in ventral portion (Fig. 93). A row of numerous setules along posterior margin at some distance from one on inner side of carapace (Figs 85, 86, 103, 104), these setules in ventral portion of posterior margin organized into groups. Ventral margin convex, but wavy due to shallow depressions in its medium and posterior portions, with 84–95 setae of different size in different regions of margin, between them series of small setules (Figs 84, 102). Last 2–4 setae short, pointed, spine-like. Antero-ventral angle rounded. Sculpture in shape of longitudal, sometimes anastomosing lines present in posterior and ventral portion of valves and anterior part of head shield.

In anterior and dorsal view, body highly compressed laterally (Figs 76, 93–95) , with rudimentary dorsal keel, maximum width of body on level of egg chamber, width evenly decreasing ventrally.

Head relatively small (Figs 77, 96, 97), not keeled in anterior view, triangle-round in lateral view, with evenly convex dorsal margin. Rostrum well developed, blunt. Eye larger than ocellus. Distance from tip of rostrum to ocellus slightly greater than that between ocellus and eye.

Head shield (Fig. 78) only slightly elongated, length about 1.5 times maximum width, its maximum width immediately behind mandibular articulation. Rostrum short, blunt. Posteriormost extremity of head shield as widely-rounded angle. Three major head pores, with narrow connection (Fig. 98). Central pore of same size as anterior or posterior one, located at middle. PP = 1.5–2 IP. Minute lateral head pores located far from main pores, about 1.5 IP distance from midline, at level of central major head pore or somewhat anteriad.

Labrum large (Figs 80–83, 99–101). Distal labral plate with only one small row of setules on each side. Labral keel broadly expanded. Ventral margin convex, wavy in most adults. Distal part of labral keel rounded in most animals, but with others with expressed, although blunt apex. Posterior margin of keel slightly convex to straight. No setulation both on anterior and posterior margin of keel. Large lateral projection in anterior (basal) portion, and small hillock in posterior (distal) portion on each side of labrum body. No special folds surrounding its base.

Thorax relatively long. *Abdomen* short, dorsal surface of segments not saddle-shaped. No abdominal projection (although anteriormost segment inflated dorsally), transverse rows of setules on each segment.

Postabdomen relatively broad, slightly narrowing distally, length about 2.7 maximum width (Figs 87–90, 105–109). Ventral margin slightly convex to straight, without groups of setules. Inflated basis of claws bordered from distal margin by obscure incision. Distal margin practically straight, broadly rounded angle between distal and dorsal margins. Dorsal margin slightly convex, with long distal part, about 3.5 times longer than preanal one, anal margin slightly longer than postanal margin too. Both preanal and postanal angles well expressed, but preanal angle specially acute. Preanal margin short, with angle-shape concavity in the middle, body wall specially chitinized in this region.

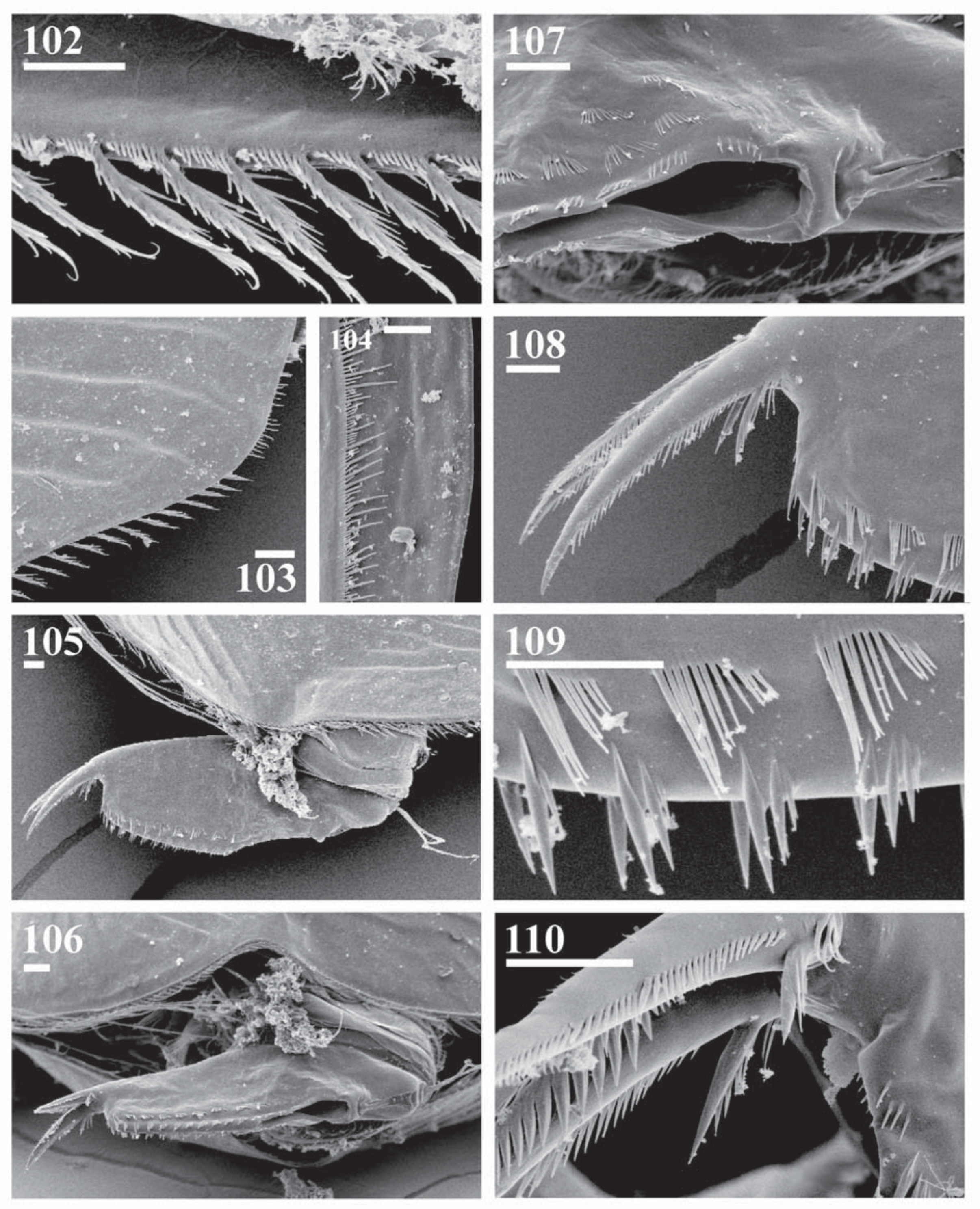
Postanal part of the postabdomen provided with 9–12 clusters of marginal denticles (Figs 89, 90, 108), the distalmost member of cluster always largest. Clusters of denticles merging into groups of marginal setules, continued on anal margin. On sides of postabdomen 12–15 lateral fascicles of relatively long (longer than denticles), delicate setules, distalmost setule of each fascicle longest; additional rows of fascicles in anal region. In some animals, fascicles of analogous, but shorter, setules on sides of postabdomen medially.

Postabdominal claw relatively short, not too robust (Figs 91, 110), much shorter than preanal portion of postabdomen, with two pectens along dorsal margin. Basal spine length ca. 0.25% of claw, armed with short setules. A bunch of setules at claw base.

Antennule relatively elongated, not reaching tip of rostrum, without any transverse rows of setules at anterior face (Figs 111, 126). Antennular sensory seta slender, arising sub-distally (relatively far from bunch of aesthetascs), shorter than antennule, but projecting markedly beyond the distal antennular end. Nine aesthetascs, three of them longer than the rest, but shorter than antennule. All aesthetascs projecting beyond tip of rostrum.

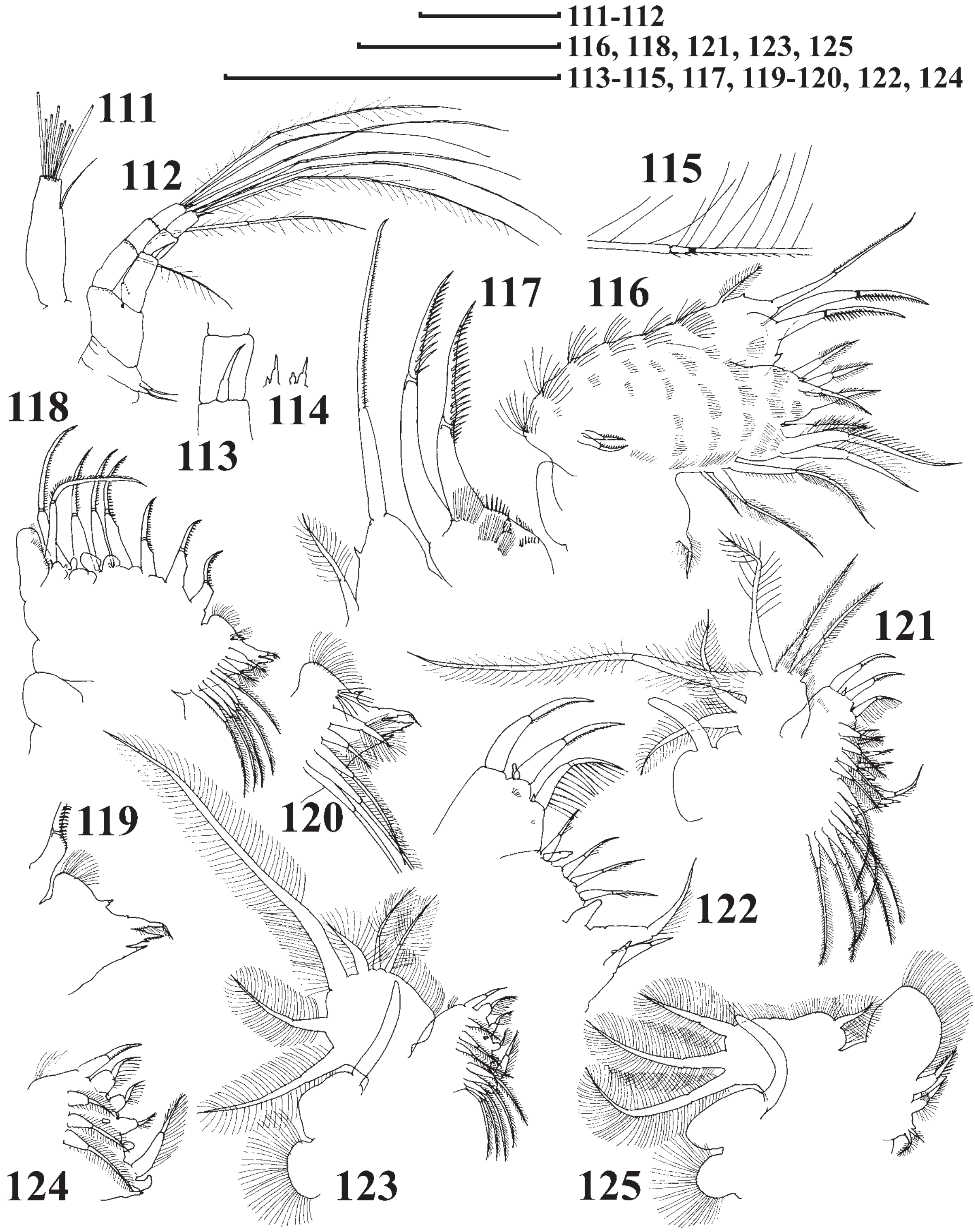
Antenna short (Figs 112–116, 127, 128). Antennal formula, setae 0-0-3/1-1-3, spines 1-0-1/0-0-1. Coxal part folded, with two sensory setae. Basal segment robust, with rudimentary seta distally. Branches relatively elongated, all segments cylindrical, with minute setules around distal margin, basal segments longest. Apical setae long for a chydorid, setulated asymmetrically. Seta arising from basal segment of endopod thin, short, but projecting beyond tip of distal segment. Seta arising from middle segment of endopod shorter than apical setae. Spine on basal segment of exopod long, only somewhat shorter than second segment. Spines on both apical segments of exopod and endopod short, with hillocks at base.

Trunk limb I large (Figs 116, 133). Epipodite ovoid, without finger-like projection. Accessory seta short, 3 times shorter than ODL setae, feathered bilaterally. ODL with one



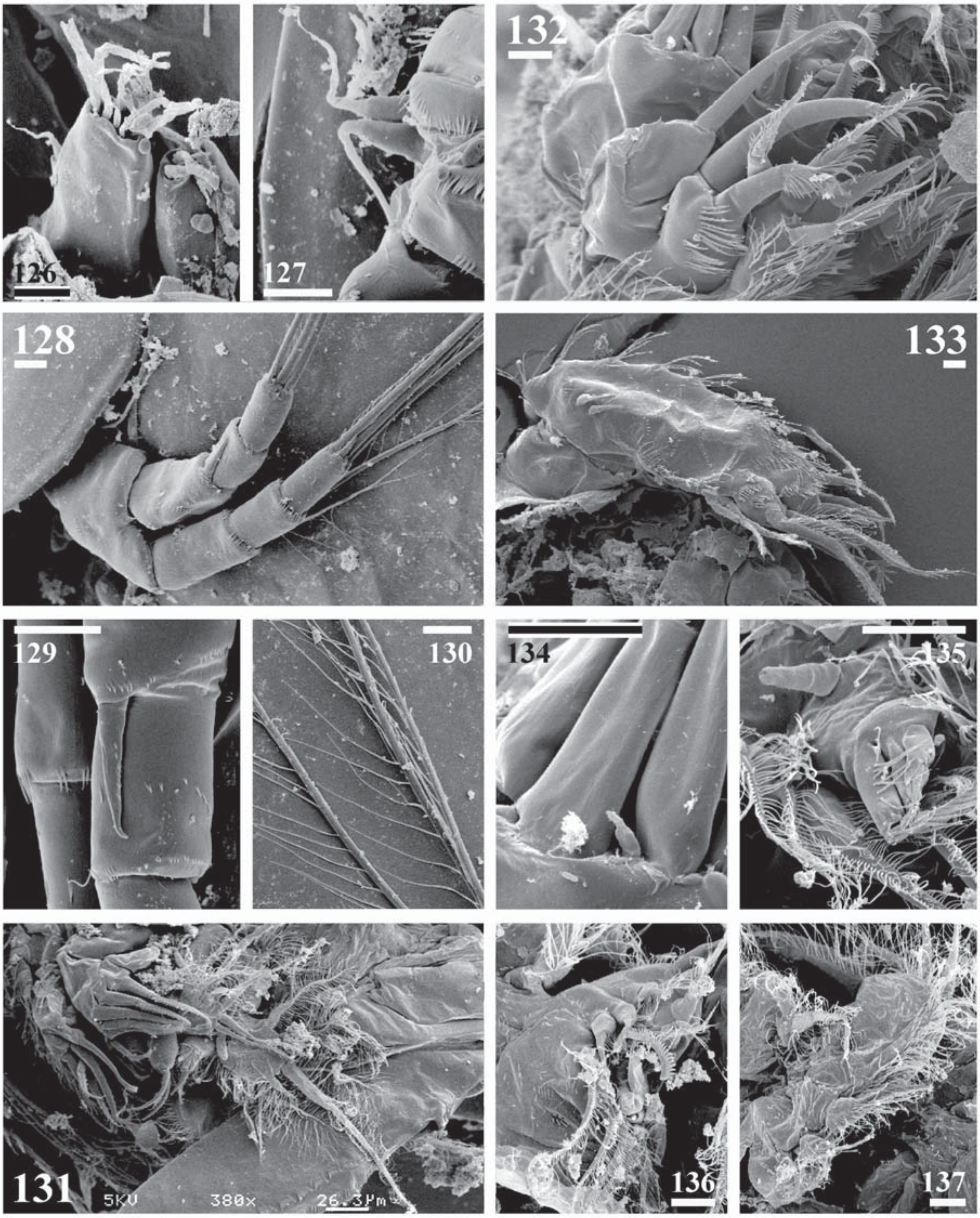
Figs 102–110. *Leberis davidi* (Richard, 1895), parthenogenetic ♀♀ from from Mexico, Chiapas, Lagos de Montebello, a small pond near Pojoj, 16.04.2000, coll. M. Gutierrez-Aguirre: 102–104 — armature of ventral, postero-ventral and posterior margin of valve; 105, 106 — postabdomen in lateral and dorsal view; 107 — region of anus; 108 — distal portion of postabdomen; 109 — postanal margin; 110 — postabdominal claws. Scale denote 0.01 mm.

Рис. 102–110. *Leberis davidi* (Richard, 1895), партеногенетические ♀♀ Мексика, Чапас, Lagos de Montebello, небольшой пруд в окрестностях Pojoj, 16.04.2000, колл. M. Gutierrez-Aguirre: 102–104 — вооружение нижнего, заднее-нижнего и зажнего края створки; 105, 106 — постабдомен латерально и дорсально; 107 — область ануса; 108 — дистальная часть постабдомена; 109 — его постанальный край; 110 — коготки постабдомена. Масштаб 0,01 мм.



Figs 111–125. *Leberis davidi* (Richard, 1895), head and thoracic appendages of parthenogenetic ♀♀ from from Mexico, Chiapas, Lagos de Montebello, a small pond near Pojoj, 16.04.2000, coll. M. Gutierrez-Aguirre: 111 — antennula; 112, 113 — antenna and spine on basal segment of its exopod; 114 — terminal spines of exopod and endopod; 115 — swimming seta; 116, 117 — limb I and its distal portion; 118–120 — limb II and its gnathobase; 121, 122 — limb III and its inner portion; 123, 124 — limb IV and its inner portion; 125 — limb V. Scale denote 0.1 mm.

Рис. 111–125. *Leberis davidi* (Richard, 1895), головные и торакальные конечности партеногенетических ♀♀ Мексика, Чапас, Lagos de Montebello, небольшой пруд в окрестностях Pojoj, 16.04.2000, колл. M. Gutierrez-Aguirre: 111 — антеннула; 112, 113 — антенна и шип базального сегменте ее экзоподита; 114 — апикальные шипы ветвей антенны; 115 — плавательная щетинка; 116, 117 — нога I и ее дистальная часть; 118–120 — нога II и ее гнатобаза; 121, 122 — нога III и ее внутренняя часть; 123, 124 — нога IV и ее внутренняя часть; 125 — нога V. Масштаб 0,1 мм.



Figs 126–137. *Leberis davidi* (Richard, 1895), parthenogenetic ♀♀ from Mexico, Chiapas, Lagos de Montebello, a small pond near Pojoj, 16.04.2000, coll. M. Gutierrez-Aguirre: 126 — antennula; 127 — coxal part of antenna; 128 — antenna and its branches; 130 — swimming seta; 131 — thoracal limbs; 132 — distal portion of limb I; 133 — limb I in inner view; 134 — sensillum on limb II; 135 — gnathobase III; 135, 136 — inner portion of limb IV and V. Scale denote 0.01 mm.

Рис. 126–137. *Leberis davidi* (Richard, 1895), партеногенетические ♀♀ Мексика, Чапас, Lagos de Montebello, небольшой пруд в окрестностях Pojoj, 16.04.2000, колл. M. Gutierrez-Aguirre: 126 — антеннула; 127 — основание антенны; 128 — ветви антенны; 130 — плавательная щетинка; 131 — торакальные ноги; 132 — дистальная часть ноги I; 133 — нога I изнутри; 134 — сенсилла ноги II; 135 — гнатобаза ноги III; 135, 136 — внутренняя часть ног IV и V. Масштаб 0,01 мм.

long, bisegmented seta, distal segment with unilateral setules, and a small hillock. IDL with two setae of unequal length, both armed with hard setules in distal part. In addition to setae, a rudimentary element, and 5 clusters of setules on ventral face of IDL (Figs 117, 132).

Endite 3 with four setae of subequal length, one of them lies anteriorly to others, a small sensillum near its base. On endite 2 three densely feathered setae, of unequal size, the longest one larger than ODL seta Endite 1 with three setae, two distalmost members long, bisegmented and setulated in distal part, third seta short and naked. Rows of thin setules on ventral face of limb. Two ejector hooks small, subequal in size. Maxillar process with one short, completely setulated seta.

Trunk limb II triangle-round (Fig. 118). Epipodite as hillock, poor expressed. Exopodite ovoid, without setae, only with rows of fine setules. Inner portion of limb ("endopodite") with eight scraping spines increasing progressively in length distally. Four distalmost members armed with thinner setules, than others. A deep incision between "endopodite" and gnathobase. Portion of gnathobase bordering "endopodite" somewhat inflated, and densely setulated (Figs 119, 120). Distal armature of gnathobase with four elements, one of them minute. Filter plate II with seven setae, three posteriormost members shorter than rest, posteriormost seta specially inflated.

Trunk limb III epipodite ovoid, with long finger-like projection. Exopodite sub-quadrangular (Fig. 121), setae subdivided in distal and basal group. Seta 3 long, with massive basal part, setae 4–6 two times shorter, setae 1–2 three times shorter than seta 3. Setae 1–4 feathered in distal part, setae 5–6 with short basal setules.

Distal endite with three setae. Distalmost two stout, distal segments with unilateral short setules; basalmost seta slightly shorter, unilaterally armed with long setules (Fig. 122). A small bottle-shaped sensillum near medium seta, minute element near seta 3 too. Basal endite with four setae, slightly increasing in size in length in basal direction, all distally with short setules. Four soft setae increasing in size basally. Gnathobase unclearly separated from basal endite (Fig. 135). Distal armature of gnathobase with four elements. The first one elongated, bottle-shaped sensillum, second long, but thick seta, third and fourth elements are spines. Filter plate III with seven subequal setae, all with similar setulation.

Trunk limb IV. Pre-epipodite setulated, epipodite ovoid, with long finger-like projection. Exopodite trapezium-shaped, with six setae (Fig. 123), the general pattern of their location similar to that of limb III, but armed in different manner. Seta 3 very long, seta 1 two times shorter, other setae not exceed ? length of seta 3, seta 4 being shortest. 3. Setae 1–4 feathered by long setules, setae 5–6 with short setules in distal part. "Endopodite" IV with four marginal setae (Figs 124, 135). Distalmost seta stout, with short setules distally, three others with inflated basal segments and slender, setulated distal segments. An element (sensillum?) near seta 3. Three soft setae with size increasing basally. Gnathobase with one globular sensillum, medium-sized bisegmented setae, and short rudimentary seta. Filter plate with five setae.

Trunk limb V. Pre-epipodite ovoid, setulated. Epipodite ovoid, with long, curved finger-like projection (Fig. 125). Exopodite with unclearly subdivided lateral margin, lateral group with three densely setulated setae, a single distal short seta. Inner limb portion an elongated lobe, with setulated inner margin (Fig. 136). At inner face, two densely setulated setae, distalmost one somewhat larger. Filter plate with two setae.

Ephippial female. Smaller ephippial female similar in shape to parthenogenetic females, larger specimens with more high body and irregular dorsal margin of valves, almost straight in posterior half of body. Ephippium yellow-brown, covered by prominent polygonal sculpture.

Male. Body shape of instar I and instar II males similar to that of juvenile females of same instar, but somewhat lower (Figs 64, 140, 145). Adult male only a little larger than instar II male, of same proportions (Figs 64, 65). Major head pores of adult male located closely to the posterior margin of head shield, PP about 0.5 IP (Fig. 67).

Postabdomen in instar I, similar to that of female, with sperm ducts opening at middle of ventral margin (Figs 141, 142). In instar II (Figs 146, 147), sperm duct openings located closely to base of postabdominal claws, with a notch after them, angle between distal and dorsal margins of postabdomen almost right. Postabdomen of both juvenile instars armed with same marginal denticles as female postabdomen (see Fig. 139), with postabdominal claws resembling those of female. In adult male, postabdomen more narrow than in female (Figs 68–70), dorso-distal angle of it varies from well-defined, similar to that of female to almost absent, broadly rounded. Both postanal and preanal angles weakly defined. Sperm ducts openings located straight above the base of postabdominal claws. Clusters of short setules located in place of female marginal denticles. Postabdominal claws considerably shorter than that of female, but the length of basal spine remains the same as in female. Setulation of claws and spine same as in female.

Antennule in instar I, same as in female, with nine aesthetascs only (Fig. 143). In instar II (Fig. 148), antennule with rudimentary male seta, with nine aesthetascs only, but differences in size between them remarkably smaller than in female. In adult male, with nine terminal aesthetascs and two lateral aesthetascs under the base of male seta (Fig. 71) . Male seta well-developed, about one-third length of antennule.

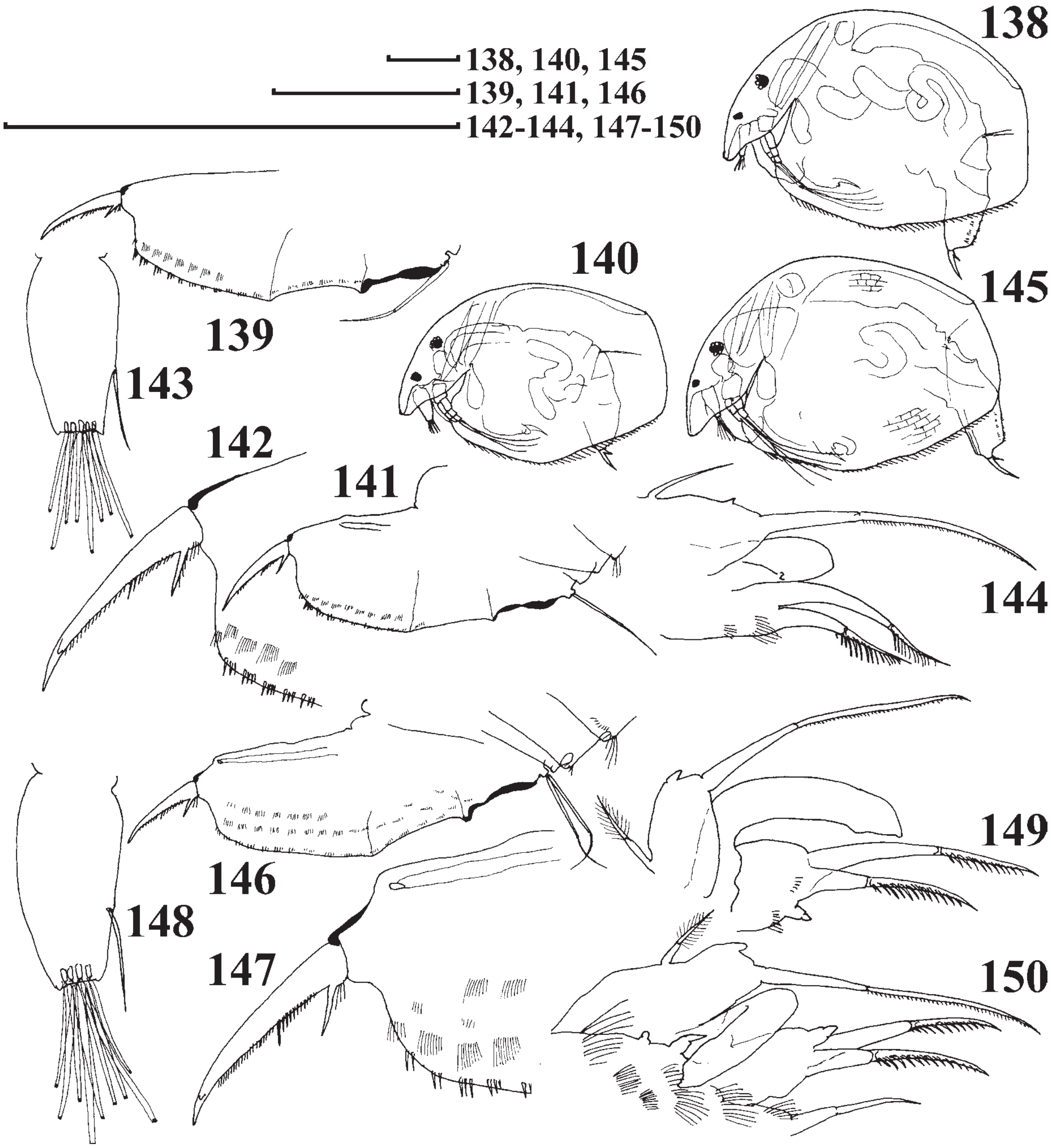
Trunk limb I in instar I (Fig. 144), copulatory hook short and stout, IDL of same structure as in female. In instar II (Figs 149, 150), copulatory hook curved, IDL with anlage of male seta, ventral face of limb with anlage of copulatory brush seta. In adult male (Figs 72–74) copulatory hook U-shaped, with free arm little longer than its base, IDL with male seta shorter than both IDL setae, copulatory brush setae of about two third length of male seta. Row of 25–30 long, hard setules on ventral face of limb, continuing from copulatory brush to first seta of endite 3.

SIZE. Length of juvenile ♀ from 0.34 mm, length of adult ♀ 0.53–0.67 mm, length of adult ♂ 0.44–0.52 mm.

VARIABILITY. Shape of labral keel varies greatly variable, its posterior margin convex or wavy (a shape never observed in *L. diaphanus*). In most populations, majority of adults with wavy margins, but in Sars' samples from Argentina only few specimens with wavy margins. Degree of development of sculpture on valves varies between specimens; in most it is unseen under the optical microscope unless it is dried. Variability of antennule, antenna, and trunk limbs minimal.

Discussion

Our data show that *L. diaphanus* and *L. davidi* are separate species, and once again a previously cosmopolitan "species" of Aloninae is revealed to be a complex of geographically distinct species. Characters that separate these two are numerous (see Table 1) and



Figs 138–150. *Leberis davidi* (Richard, 1895), juvenile ♀♀ and ♂♂ from Mexico, Chiapas, Lagos de Montebello, a small pond near Pojoj, 16.04.2000, coll. M. Gutierrez-Aguirreo: 138, 139 — juvenile ♀ and its postabdomen; 140–144 — juvenile ♂ of instar I, its postabdomen, antennula and limb I; 145–150 — juvenile ♂ of instar II, its postabdomen, antennula and limb I. Scale denote 0.1 mm.

Рис. 138–150. *Leberis davidi* (Richard, 1895), ювенильные ♀♀ и ♂♂, Мексика, Чапас, Lagos de Montebello, небольшой пруд в окрестностях Pojoj, 16.04.2000, колл. M. Gutierrez-Aguirre: 138, 139 — ювенильная ♀ и ее постабдомен; 140–144 — ювенильный ♂ первого возраста, его постабдомен, антеннула и нога I; 145–150 — ювенильный ♂ второго возраста, его постабдомен, антеннула и нога I. Масштаб 0,1 мм.

include differences in size, IP/PP ratio, number of ventral setae of valves and trunk limb morphology.

The revision of the *diaphanus*-group has only just begun, and many new questions arise. The taxonomic status of *A. punctata* Daday, 1905 described from Shri-Lanka, is unknown; and the status of *diaphanus*-group populations in Tropical Asia, Africa and South Europe remains uncertain. We can speculate with a degree of certainty that *L. davidi* s. str. is not present in the Old World, but the question of the distribution of *L. diaphanus* is open, and it is unclear whether it is an Australian endemic or not. Furthermore, it is impossi-

Table 1. Main differences between *L. diaphanus* and *L. davidi.*
Table 1. Основные различия между видами *L. diapanus* и *L. davidi.*

Character	*L. diaphanus*	*L. davidi*
Size of female	up to 0.57 mm	up to 0.69 mm
Ventral margin of valves	with 58-67 setae	with 84-95 setae
Location of major head pores	PP less than 1 IP	PP=1.5-2 IP
Anterior margin of labrum	always convex	frequently wavy
Seta of basal segment of exopod of antenna	longer than second segment	shorter than second segment
Accessory seta of limb I	long, two times shorter than ODL seta	short, three times shorter than ODL seta
Exopodite III	seta 5 longer than seta 6	setae 5 and 6 of same length
Exopodite IV	seta 3 of moderate length, seta 5 longer than seta 6	seta 3 very long, setae 5 and 6 of same length
Epipodites III-V	without finger-like projections	with long finger-like projections

Table 2. Main morphological differences between species of the *diaphana*-group, *A. quadrangularis* (type species of *Alona*) and European species of *Alona.*
Таблица 2. Основные различия между видами группы *diaphana*, *A. quadrangularis* (типовым видом рода *Alona*) и европейскими видами рода *Alona.*

Character	Species of *diaphana*-group	*Alona quadrangularis*	European species of *Alona*
Body in lateral view	ovoid	irregular elongated, widening distally	oval or irregular, never ovoid
Ventral margin of valves	convex	straight	straight, never convex
Dorsal keel	present	absent	always absent
Rostrum	truncated, blunt	broadly rounded	always broadly rounded
Number of major head pores	three	three	three or two (in *A. affinis, A. intermedia)*
Denticles of postabdomen	clusters of small denticles	large single denticles with spinules on anterior margin	usually large single denticles with spinules on anterior margin; if denticles in clusters, posteriormost member considerably larger than others
IDL	with 2 setae	with 3 setae	usually with 3 setae (2 setae in *A. rectangula*)
Exopodite II	without seta	with well-developed seta	always with seta
Exopodite III	with 6 setae	with 7 setae	usually with 7 setae (6 setae in *A. rectangula*)

ble to evaluate the status of *A. davidi vermiculata*: in its present meaning it can be anything, from a variety of *L. diaphanus* to a separate species.

Our decision to remove species of the *diaphana*-group from the genus *Alona* is based on the differences summarized in Table 2. The only character in common with *Alona quadrangularis* (O.F. Müller, 1785) is the possession of three main head pores.

The relationship between the *diaphana*-group and genera *Leberis* and *Celsinotum* was discussed by Frey [1991], who pointed out numerous similarities between *A. diaphana* and *Celsinotum,* but concluded that it does not belong to this genus.

In reality, the *diaphana*-group and *L. aenigmatosa* share numerous characters. They have a dorsal ridge or keel on the carapace, but not on the head shield, while the majority of Aloninae lack such a structure. Only three genera of Aloninae – *Celsinotum*, *Acroperus* and *Camptocercus* have a keeled carapace. In the latter two, the keel extends to the head shield. The blunt,

Table 3. Differences between *L. aenigmatosus* and species of *diaphana*-group.
Таблица 3. Различия между *L. aenigmatosus* и видами группы *diaphana*.

Character	*L. aenigmatosus* (from Frey, 1998)	species of *diaphana*-group
Size	large for subfamily (up to 1.1 mm)	medium for subfamily (less than 0.7 mm)
Dorsum	with weak ridge	with more or less developed keel
Posterior margin of head shield	triangular, with straight sides converging to a narrowly-rounded tip.	with broadly rounded tip and curving sides
Location of major head pores	PP = 3-4 IP	PP up to 2 IP
Postabdomen	with convex distal margin evenly passing into dorsal with no clearly defined dorso-distal angle	with distal margin practically straight, perpendicular to vental one, and well-developed dorso-distal angle
Dorsal margin of postabdomen	with clusters of marginal setae in place of denticles	with groups of denticles, passing into groups of setae
IDL setae	with weakly-developed, hair-like setules in distal part	with well-developed hard setules in distal part
Gnathobase filter plate II	posteriormost seta short, all others setae considerably longer	two posteriormost setae subequal in length, considerably shorter than others

truncated rostrum is also rare character in the subfamily, where the majority of species have either a broadly rounded or elongated rostrum. Such a shape of rostrum is only found in *Celsinotum* and *Euryalona*.

Other similarities include the compressed ovoid body with convex ventral margin; the shape of the postabdomen in both sexes; similar armament of the postabdomen, with clusters of marginal denticles; the similar proportions of the antennal segments, with the basal segment of both branches 1.5 times longer than the middle and distal segments; two well-developed IDL setae; lack of a seta on exopodite II; exopodite III with six setae; and lack of a trunk limb VI. Differences in trunk limb morphology between the *diaphana*-group and *L. aenigmatosus* [see Frey, 1998] are minor, of a level observed between species in small genera, like *Karualona, Kozhowia* and *Armatalona* [Dumont & Silva-Briano, 2000; Kotov 2000; Sinev, 2004], or within species groups within *Alona* [Sinev, 1997, 2000, 2001a,b].

All differences between the *L. diaphanus*-group and *L. aenigmatosus* are at the species level (see Table 3). Their difference in size, while uncommon, is not really unusual, and is observed in several other genera of Aloninae. In *Camptocercus* for example, the maximum size of female varies from 0.7 mm in *C. fennicus* Stenroos, 1898 and *C. aloniceps* Ekman, 1901 to 1.25 mm in *C. rectirostris* Schoedler, 1862 [Smirnov, 1998]. Several other differences like PP/IP ratio and number of ventral setae on valves, correlated with size, are not genus–level characters either.

A prominent difference between the *diaphanus*-group and *L. aenigmatosa* is the degree of development of the dorsal keel: it is rather well developed in the *diaphanus*-group, but weak in *L. aenigmatosa* (see Fig. 2).

The move of the *diaphana*-group to *Leberis* also clarifies the relationship between *Leberis* and *Celsinotum*. Indeed, both *Leberis* and *Celsinotum*, according to Smirnov [1989] and Frey [1991], seem to derive from the *A. diaphana*-clade because of its primitive characters. In some characters, such as dorsal keel development and lateral compression of the body, the *A. diaphana*-group is intermediate between *L. aenigmatosus* and *Celsinotum*. Thus, specialisation of *L. aenigmatosa* lead to a reduction of the dorsal keel; in *Celsinotum*, conversely, specialisation lead to an extreme development of this character. Such evolution in an opposite direction is not to be accepted without strong evidence.

Now this situation is more easily explained. *Leberis-Celsinotum* is a monophyletic clade of Aloninae, and its main apomorphy is the presence of a dorsal ridge or keel on the valves, but not on head shield. The primitive state of this dorsal ridge is present in *L. aenigmatosus*, while in other species the keel is more developed. We expect that separation of *Celsinotum* from *Leberis*-like ancestors took place during adaptation to the extreme conditions of the temporary saline water bodies of Australia, and lead to an extreme development of the head shield. In this view, *Leberis* is the more primitive and widely distributed genus, and *Celsinotum* is specialised for extreme habitats.

A question we are not yet ready to answer is the relationship and place of *Leberis* and *Celsinotum* within the subfamily. The genus *Alona* is apparently not closely related to them and to clarify relationships with other genera we need future investigations. Finding *Celsinotum*-like animals in Amazonia [Smirnov & Santos-Silva, 1995] raises new questions in the systematics of this clade of Aloninae.

Recently, a series of new *Alona*-like genera was established [Rajapaksa & Fernando, 1987; Smirnov, 1989; Frey, 1991; Ciros-Pérez & Elías-Gutiérrez, 1997;

Chiambeng & Dumont, 1999; Dumont & Silva-Briano, 2000; Sinev, 2004]. The taxonomy and phylogeny of taxa within the Aloninae is therefore far from stable, and a redefinition of "true *Alona*" is urgently needed.

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